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KARAFIT, Steven James

PERMINERALIZED LATE CRETACEOUS PLANTS FROM THE EDEN MAIN FOSSIL LOCALITIES, BRITISH COLUMBIA, ...

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Quotes

"The small part of ignorance that we arrange and classify we give the name of knowledge."-A. Bierce

"I love fools' experiments. I am always making them."- C. Darwin

"Spend it foolishly."- J. S. Karafit

"When the center is in the middle, you have a cross section." - G. W. Rothwell

"It's not "breaking up", it's a fossil, it's just sitting there."- R. A. Stockey

"It takes a long time to pick up after a glacier."- L. E. Thompson

"No way of thinking or doing, however ancient, can be trusted without proof."
- H. D. Thoreau

There should be no monotony
In studying your botany;
It helps to train
And spur the brain--
Unless you haven't gotany...
- B. Braley

Über allen Gipfeln
Ist Ruh,
In allen Wipfeln
Spürest du
Kaum einen Hauch;
Die Vögelein schweigen im Walde,
Warte nur, balde
Ruhest du auch.
- Goethe

University of Alberta

Permineralized Late Cretaceous plants from the Eden Main fossil localities, British Columbia, Canada

by

Steven James Karafit ©

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in

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Dedication

To my family, friends, and colleges

Abstract

Permineralized fossil remains of ?dinoflagellates, mosses, ferns, gymnosperms and angiosperms have been found in calcium carbonate concretions from the Eden Main fossil localities, British Columbia, Canada. Fossils come from the Upper Cretaceous Comox Formation of the Nanaimo Group and have been dated as Coniacian in age. A survey of the fossil floral assemblage has revealed morphotaxa of eleven seedless vascular plants from stipes and rhizomes. A new species of *Paralygodium*, a schizaeaceous fern, is described from fertile pinnules. Seven gymnosperm organs are known including a cycadophyte stem, cupressaceous leaves, twigs and cones, and pinaceous leaves and a pollen cone. Twenty-five angiosperm morphotaxa are also currently recognized based on flowers, inflorescences, fruits, and wood. The presence of several taxa with extant relatives that are currently found in the tropics, and abundant fusain indicates that western North America was warm during the Coniacian, probably experienced wet and dry seasons.

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Chapter 1

Introduction

The Eden Main fossil localities contain a rich assemblage of anatomically-preserved terrestrial plant (Mindell et al., 2006a; Karafit and Stockey, 2008) and marine animal fossils (Haggart et al., 2003; Schweitzer et al., 2003). The purpose of this thesis is to provide a preliminary overview of the Late Cretaceous (early Coniacian) fossil floral assemblage of the Eden Main fossil localities located on Vancouver Island, British Columbia, Canada.

Anatomically preserved plants from the Coniacian are not common in the fossil record and only a few sites are known. These include: permineralized podocarpaceous woods found off the coast of South Africa (Bamford and Stevenson, 2002); permineralized plants from Hokkaido, Japan that span the Turonian-Campanian (?Maastrichtian) (e.g., Nishida, 1991), mesofossils from the early Coniacian Kamikitaba locality, Japan (Takahashi et al., 1999a, 1999b, 2001, 2002) and Coniacian-Santonian mesofossils from Georgia, U.S.A (Magallón-Puebla et al., 1997). Most of the mesofossils known from these localities are preserved as fusain (fossil charcoal) (Crane and Herendeen, 1996; Frumin and Friis, 1996; Magallón-Puebla et al., 1997; Takahashi et al. 1999, 2001, 2002; Eklund, 2003; Schönenberger, 2005), that is also common in the concretions from the Eden Main localities described in this thesis. Fusain provides some clues about paleoclimate, ecology and, since the transport of modern charcoal is well understood, information on transportation and deposition of fossil plant material may also be interpreted (e.g., Jones and Chaloner, 1991; Scott, 2000; Scott et al., 2000).

Significance

The early Late Cretaceous was an important time of vegetational change. Many angiosperm families with extant taxa were already present (e.g., Crane, 1987.). Ferns from the second evolutionary radiation (Permian-Cretaceous) were declining in numbers and the third radiation was taking place (Lovis, 1977; Crane, 1987; Rothwell, 1987). The global dominance of gymnosperms was gradually declining as flowering plants diversified in the Cretaceous and began to compete with existing vegetation; flowering plants out competed some groups and opened new niches for others (Schneider et al., 2004).

Many Late Cretaceous fossil localities contain compression/impression fossils that are informative, but only allow a limited comparison to extant taxa. However, fossils at the Eden Main localities display three-dimensional cellular preservation. This preservation allows for detailed comparison to extant taxa (when anatomy of extant taxa is known), and other anatomically preserved plants. Furthermore, potential to reconstruct the plants in three dimensions allows comparison of the morphology to other fossil remains preserved by various modes of preservation. The classification of fossil plants and examination of closely related extant plants can lead to a better understanding of the ecology of fossil plants as well as the climate in which they grew. However, caution must be taken when trying to determine the habitats from which the plants from Eden Main came, because it is not possible to know if the fossil plant remains at the localities originate from one geographic area or if they represent a collection of plants from various areas that were mixed together in the marine environment prior to deposition.

Material and Methods

Fossil plants were collected at the Eden Main localities on Vancouver Island. These localities are approximately 35 kilometers northwest of Comox, British Columbia, Canada (Fig.1). The localities are accessed from the Cranberry Lane exit of Inland Island Hwy. (19), 2 km to the Oyster River Main Logging Road gate, then 9.5 km on Oyster River Main to Eden Main Logging Road (Fig. 2) (Schweitzer et al., 2003). Several outcrops have been collected including a quarry, referred to in the text as "Eden Quarry"; a roadside ditch along the Eden Main logging road, a.k.a. Eden Creek (Schweitzer et al., 2003); referred to in the text as "the Ditch", a roadside ditch alongside the "Eden 400" logging road, an exposure along "Eden Creek", and a second roadside ditch along the Eden Main logging road referred to as the "2nd Ditch" in the text (Table 1; Fig. 2). Permineralized plant remains occur along with mollusc shells, bone fragments and pyrite in calcium carbonate concretions found in shallow marine or near marine sandstone deposits of the Dunsmuir Member of the Comox Formation of the Nanaimo Group (Haggart et al. 2003) (Fig. 3). The Nanaimo Group is economically important because coal seams are mined in some areas (e.g., Kenyon et al., 1992).

The Comox Formation has traditionally been recognized as Santonian in age (e.g., Muller and Jeletzky, 1970; Bickford and Kenyon, 1988; Kenyon et al., 1992). However, the Eden Main localities have been dated as late Turonian to early Coniacian using mollusc index fossils (Haggart et al., 2003). The fossils from Eden Main are most likely early Coniacian in age (J. Haggart; D. Meckert, personal communication, 2006). Other outcrops nearby, on the Gulf Islands of B.C. and the San Juan Islands of Washington State, have been identified as Turonian in age (Haggart, 1991, 1994; Haggart et al.,

2005). Haggart (1994), and Haggart et al. (2005) suggested the formation at these island sites is not the Comox but the Sidney Island Formation. However, Johnstone et al. (2006) argued that due to similar lithology and sedimentology on Vancouver Island, and on the Gulf and San Juan Islands, the Comox Formation should still be applied to these locations. The Comox Formation is of a diachronous nature, spanning the late Turonian to early Campanian (Mustard, 1994; Johnstone et al., 2006).

Over 200 concretions from 0.5 to 20 cm in diameter, were cut into serial sections and studied using the cellulose acetate peel technique (Joy et al., 1956). Concretions are common at the Eden Main localities and often contain abundant plant and animal remains. It has been suggested that calcium carbonate concretions form in the presence of sulfur-reducing bacteria which feed on decaying plant or animal material and create a microenvironment in which calcium carbonate is precipitated (e.g., Raiswell and Fischer, 2000). The presence of pyrite framboids (Popa et al., 2004) in fossils at Eden Main may support this theory. Sulfur-reducing bacteria produce hydrogen sulfide (HS) which may react with suspended iron in the seawater, producing pyrite framboids (Popa et al., 2004).

Specimens were mounted on slides using Eukitt xylene-soluble mounting medium (O. Kindler GmbH, Freiberg, Germany). Images were captured using a PowerPhase digital scanning camera (Phase One A/S, Copenhagen, Denmark) and processed using Adobe Photoshop 7.0. Three dimensional reconstructions were created with AMIRA 3.1.1 (TGS Template Graphics Software, San Diego, Calif.) computer visualization software.

Fusain was also examined with the cellulose acetate peel technique. In addition, fusain and plant cuticle were extracted by dissolving a piece of concretion in 5% HCL

and removing remaining plant material with a paintbrush or pipette.

Spores and pollen were prepared for scanning electron microscopy (SEM) by dissolving the acetate peels bearing specimens using a modified Daghlian and Taylor (1979) technique with acetone on a Millipore Filter (Millipore, Bedford, MA). Filter paper with the resulting spores or pollen was then mounted on stubs with double sticky tape. Spores were coated with 100 Å Au using a Nanotek Sputter Coater and examined with a JEOL 6301F SEM at 5 kV. All specimens are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA) Edmonton, Alberta, Canada.

The Present Work

In this work I provide an overview of the possible dinoflagellates, mosses and ferns found at the Eden Main localities (Chapter 2). I describe a new species of *Paralygodium*, a schizaeaceous fern, from fertile pinnules (Chapter 3). I also describe numerous fossil vegetative and reproductive conifer and angiosperm organs, and compare them to other extant and fossil taxa (Chapter 4). The order in which fern taxa are presented is based on the classification of Hasebe et al., 1995. Seed plant taxa are organized according to APG II (Angiosperm Phylogeny Group, 2003).

Table 1. Eden Main localities

Site	Name	Lattitude and Longitude
1	Eden Quarry	49°49'52.04"N, 125°25'10.41"W
2	The Ditch	49°49'39.40"N, 125°25'43.50"W
3	Eden 400	49°49'38.12"N, 125°26'22.08"W
4	Eden Creek	49°49'27.74"N, 125°26'32.33"W
5	2nd Ditch	49°49'24.02"N, 125°26'51.02"W

Figure 1

Map of Vancouver Island showing Eden Main localities (modified from Hernandez-Castillo et al., 2006).

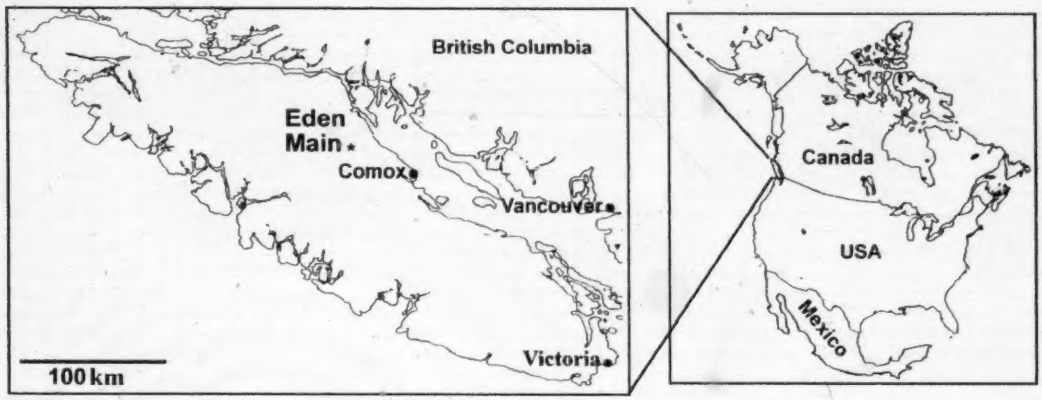

British Columbia
Eden
Main
Comox
Vancouver
Victoria
100 km
Canada
USA
Mexico

Figure 2

Geological map of Eden Main localities showing location of Eden Quarry (1), Eden Ditch (2), Eden 400 (3), Eden Creek (4) and the 2nd Ditch (5) (modified from P.S. Mustard, 2008, unpublished figure).

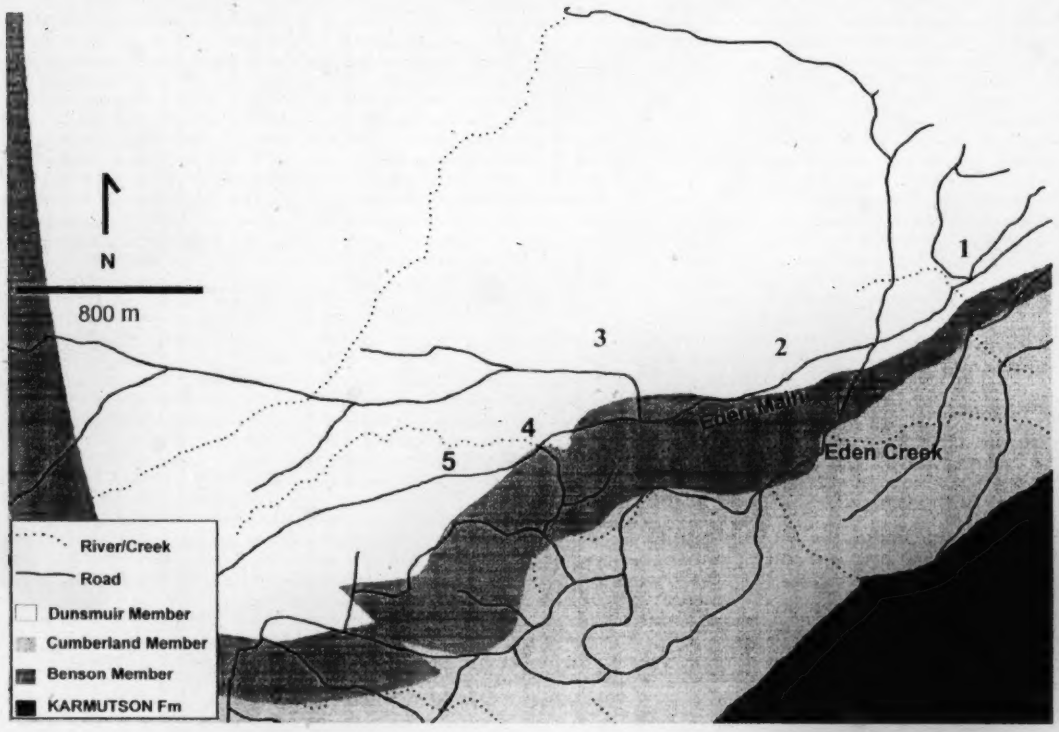
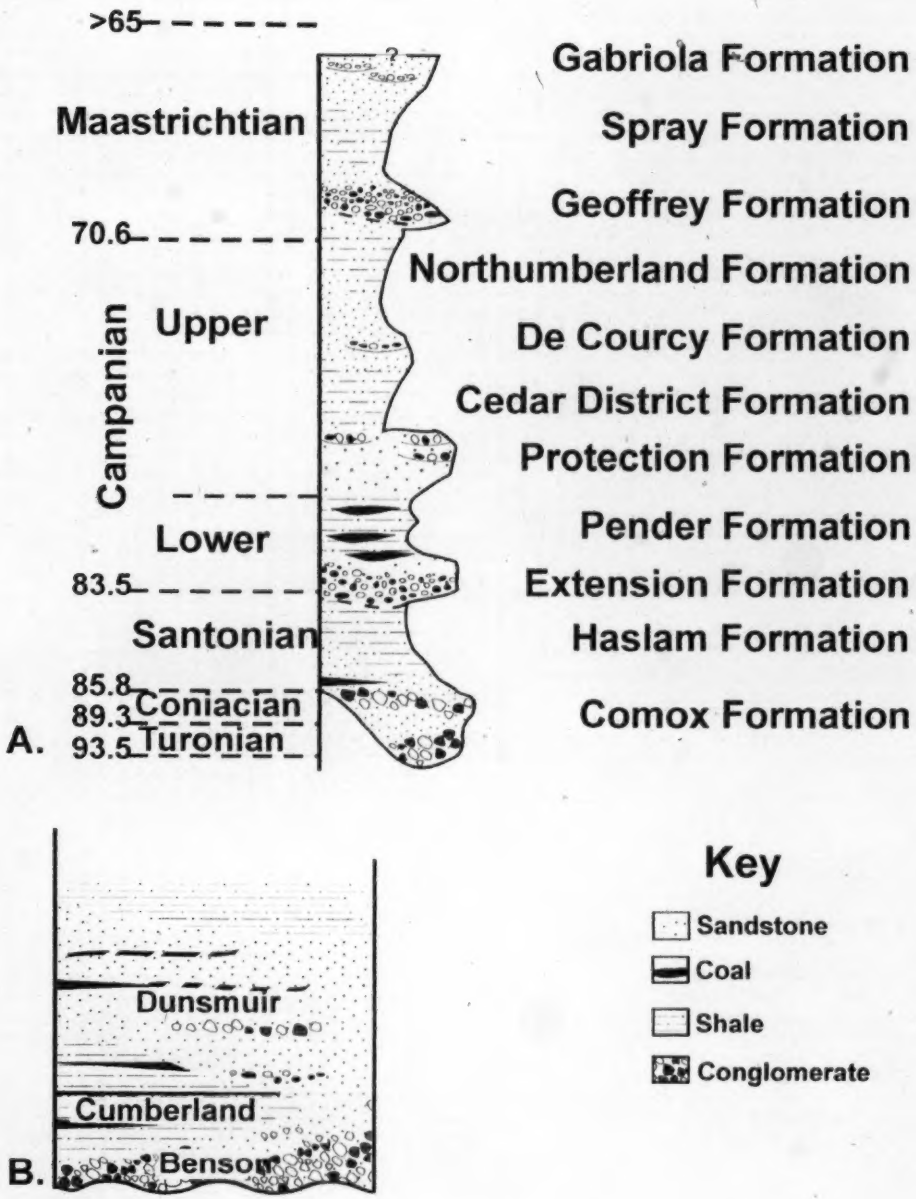

N
800 m
1
2
3
4
5
Eden Main
Eden Creek
River/Creek
Road
Dunsmuir Member
Cumberland Member
Benson Member
KARMUTSON Fm

Figure 3

(a) Generalized lithostratigraphy of Nanaimo Group (modified from Johnstone, 2006 after Mustard, 1994). (b) Generalized stratigraphy of members of Comox Formation (Modified from Johnstone et al., 2006 after Bickford and Kenyon 1988; and Mustard 1994).


>65
Maastrichtian
70.6
Campanian
Upper
Lower
83.5
Santonian
85.8
89.3
Coniacian
93.5
Turonian
A.
Gabriola Formation
Spray Formation
Geoffrey Formation
Northumberland Formation
De Courcy Formation
Cedar District Formation
Protection Formation
Pender Formation
Extension Formation
Haslam Formation
Comox Formation
Dunsmuir
Cumberland
Benson
B.
Key
Sandstone
Coal
Shale
Conglomerate

Chapter 2

Eden Main Flora: Seedless taxa

Introduction: In this chapter I will describe the protists, mosses and seedless vascular plants (pteridophytes) found in the Eden Main concretions. Many of these taxa are only known from a few specimens. The most common seedless plants at the sites are from the fern family Gleicheniaceae which occur in nearly every concretion.

Kingdom: Protista

Division: ?Dinophyta

?Dinoflagellate cysts

(Plate 1, Figs. 1-2)

Description: Round cysts up to 45 µm in diameter are known from the Eden Main localities. The surface is ornamented with processes *ca* 3 µm wide and *ca* 6 µm long with branched tips (Plate 1, Figs. 1-2). Surfaces of some cysts contain angular openings (Plate 1, Fig. 1).

Occurrence: Eden Quarry: P14465 C bot and D top, inside a conifer seed.

Discussion: Small spheroidal cysts with processes found in the fossil record are often identified as acritarchs or dinoflagellate cysts (Traverse, 2007). Both may occur as marine fossils and can be difficult to distinguish from one another (Evitt, 1963). Acritarchs are of unknown affinities, their bodies are not composed of paraplates, while dinoflagellate cyst bodies display paratabulation (arrangement of paraplates is discernable) (Sarjeant et al., 1987; Moldowan and Talyzina, 1998). The angular openings in the walls of the Eden Main cyst may be archeopyles (excystment apertures) and their angular nature suggest that the cyst bodies are composed of paraplates, and

therefore, these structures are probably dinoflagellates (Vera Pospelova personal communication, 2008) even though paratabulation of the cyst wall has not been observed.

The record of dinoflagellate cysts begins as early as the Triassic (Powell, 1992; Traverse, 2007) but some evidence suggests they had evolved by the Neoproterozoic (Butterfield and Rainbird, 1998). The Eden Main cysts appear to be proximochorate (processes length is 10-30 % of cyst diameter) with trifurcate or orthogonal processes (Matsuoka and Fukuyo, 2000). It should be noted that some ascomycete fungi (Castellano et al., 1989) and oomycetes (Domsch et al., 1980) have spores of similar size and morphology as the Eden Main fossils, however, the processes of the fungal spores do not possess branched tips (Castellano et al, 1989; Domsch et al., 1980). These fossils could also be invertebrate eggs, which are easily confused with dinoflagellate cysts or acritarchs (Martin, 1993). Further research such as SEM examination will be required to determine the affinities of these cysts.

Kingdom: Plantae

Division: Bryophyta

Class: Bryopsida

Moss gametophytes

(Plate 1, Figs. 3-4)

Description: At least five specimens of gametophyte axes with imbricate leaves are known. Axes are up to 0.5 mm in diameter and composed of thin-walled parenchyma cells 3-7 µm in diameter (Plate 1, Figs. 3-4). The leaf lamina is unistratose but at the costa the leaf is one to *ca* 3-4 cells thick (Plate 1, Fig. 4). All known specimens are intact, but histology is poorly preserved.

Occurrence: Eden Quarry: P14335 B top; P14345 E top; P14347 C top, E bot; P14460 F bot; P14560 B bot.

Discussion: Unistratose, imbricating leaves are found in the Bryophyta (mosses) or some members of the Marchantiophyta (liverworts) (Schofield, 1985). However, unlike the Eden Main fossil, leaves of liverworts lack a costa (Schofield, 1985; C. LaFarge personal communication, 2007). A combination of leaf characters, e.g., leaf shape in transverse section, the presence of a costa, lack of incrassate (thickened) laminal cell walls and lack of lamellae on the costa (elongate flaps of tissue on the abaxial surface of the costa), suggest that this moss belongs in the Bryopsida (Schofield, 1985; Crum, 2001; C. LaFarge personal communication, 2007). The costa in the fossil is wide and grades from 3-4 cells at the center to two cells thick laterally before grading into the unistratose lamina. A similar costal arrangement may be found in members of the Dicranidae (Allen, 1990; C. LaFarge personal communication, 2007).

Anatomically preserved mosses are rare in the fossil record (Smoot and Taylor, 1986; Konopka et al., 1997, 1998; Herendeen et al., 1999). Mosses are generally classified by sporophyte structure making comparisons by purely vegetative organs is difficult, but if attached sporophytes or better preserved gametophytes are found, it may be possible to classify this moss with greater certainty.

Division: Tracheophyta

Order: Filicales

Family: Gleicheniaceae

Rhizome

(Plate 2, Figs. 1, 2)

Description: One charcoalified fern rhizome with a vitalized protostele (Plate 2, Figs. 1, 2), 1.8 mm in diameter has been identified. The specimen is abraded, and the epidermis is not preserved; the cortex is up to 0.3 mm wide. The cortex is black, and composed of what appear to be small sclerotic cells, but due to burning, decay, or poor preservation, most of the cortex appears homogenous. The vitalized protostele is 1.1 mm in diameter with metaxylem tracheids 42-70 μm wide (Plate 2, Fig. 2). Smaller parenchyma cells 10-28 μm in diameter are interspersed with metaxylem tracheids (Plate 2, Fig. 1, 2). The stele has *ca* 6 lobes. Protoxylem is unknown as preservation makes it impossible to distinguish it from surrounding parenchyma cells (Plate 2, Fig. 2). Small patches of probable phloem are preserved between the xylem and the cortex, with cells 12-18 μm in diameter (Plate 2, Figs. 1, 2).

Occurrence: Eden Quarry: P14399 C bot.

Discussion: Protostelic fern rhizomes are found in the Hymenophyllaceae, Gleicheniaceae, Cheiropleuriaceae, Schizaeaceae, Azollaceae, Salviniaceae, Lindsaeaceae, Pteridaceae and Vittariaceae (Ogura, 1972: Tryon and Tryon, 1982; Little et al., 2006a). Rhizomes with lobed, vitalized protosteles are not common among extant ferns and are found only in the Gleicheniaceae (Bierhorst, 1969; Ogura, 1972; Mindell et al. 2006c). Members of this family are often found growing in open areas in tropical

habitats, on the ground, or climbing available substrate (Tryon and Tryon, 1982). Lobed steles similar to this fossil specimen have been reported in *Stromatopteris* Mett., *Dicranopteris* Bernhardi or *Gleichenia* J.E. Smith (Ogura, 1972; Mindell, 2006c). In *Gleichenia* and *Dicranopteris*, each lobe contains distinct groups of protoxylem strands, while in *Stromatopteris*, the protoxylem is indistinct (Bierhorst, 1969; Ogura, 1972). The location of protoxylem can most easily be distinguished in extant and fossil rhizomes in longitudinal section since protoxylem tracheids have helical, and metaxylem tracheids have scalariform secondary wall thickenings. Only a short length of rhizome was preserved, and it was peeled through in transverse section before a longitudinal section could be made. Transverse sections can also be useful for determining the location of protoxylem tracheids because they are generally smaller than metaxylem tracheids and their walls tend to be thicker than those of parenchyma cells. Unfortunately, cell walls in the fossil are not well preserved making it impossible to distinguish protoxylem from surrounding parenchyma. This may be due to decomposition before the rhizome was burned, or cell wall break down due to burning (Scott, 2000). Further comparison to living or fossil taxa must wait until better specimens are found.

Gleicheniaceous frond segments

(Plate 2, Figs. 3-6; Plate 3, Figs. 1-4)

Description: Segments of fronds and pinnules of gleicheniaceous frond segments, are known from the Eden Main localities (Plate 2, Figs. 3-6; Plate 3, Figs. 1-4). Non-branching segments with gleicheniaceous characters are 0.5 mm-2.2 mm in diameter and have C-shaped vascular traces with infolded adaxial hooks. Vascular tissue is surrounded by a sclerenchymatous zone up to 60 µm thick, made up of 2-3 layers of cells, each up to

45 µm wide (Plate 2, Figs. 3, 4; Plate 3, Figs. 1-4). The cortex grades from these sclerotic cells to thinner-walled cells up to 45 µm wide at the outer margin. Epidermis is missing in all specimens. Vascular traces show endarch xylem maturation (Plate 2, Fig. 5). In some specimens, xylem is constricted on the lateral sides of the trace, giving it an angular appearance (Plate 2, Fig. 3). In other specimens this is not apparent (Plate 2, Fig. 4; Plate 3, Figs. 1-4). Phloem is usually either poorly preserved (Plate 2, Fig. 4) or represented by a gap between the xylem and ground tissue (Plate 2, Figs. 3, 6; Plate 3, Figs. 1-4).

Some of the fossil frond segments branch in a pseudodichotomous, gleicheniaceous manner (Chrysler, 1943, 1944; Ogura, 1972; Mindell et al., 2006c) forming three frond segments (Plate 3, Figs. 1-4). Due to quality of preservation, the anatomy of the branching regions is not completely known, but the general pattern can be discerned. First, adaxial hooks separate from the leaf trace and form rings of vascular tissue. At more distal levels (away from the rhizome), these bundles open and join the abaxial arch (Plate 3, Fig. 1). The arch then divides into three traces in the frond (Plate 3, Fig. 2). The two lateral traces eventually separate each entering a rachis (Plate 3, Figs. 3-4). The central vascular trace probably formed a dormant bud, as it did not elongate, while the lateral traces each continued to grow, forming new segments.

Occurrence: Eden Quarry; Ditch; Eden 400 Ditch; Eden Creek; Eden Main 2nd Ditch, one of the most common fossils in the flora at the localities. Figured specimens: P14338 A; P14468 C bot; P14489 B top; P14592 A.

Discussion: Gleicheniaceae occur mostly as compression/impression fossils, are known as early as the Permian (Yao and Taylor, 1988), and are common during the Mesozoic

(Tidwell and Ash, 1994). Pseudodichotomous branching and frond anatomy found in the branching Eden Main specimens clearly allow placement in the Gleicheniaceae (Chrysler, 1943, 1944; Ogura, 1972; Mindell et al., 2006c). Like the fossils, ferns in this family also produce a dormant bud at each division of the rachis. This bud can remain inactive until damage to other parts of the frond triggers the bud to form a new frond segment (Chrysler, 1943). The C-shaped vascular trace with incurved adaxial tips and the presence of constricted lateral xylem are further evidence for gleicheniaceous affinities (Chrysler, 1943, 1944; Mindell et al., 2006c). There is only one other occurrence of anatomically preserved branching gleicheniaceous frond segments in the fossil record. These are found in Eocene deposits of the Appian Way locality, also on Vancouver Island (Mindell et al., 2006c).

Family: Schizaeaceae

Genus: *Paralygodium* Yoshida, H. Nishida et M. Nishida (1997)

Paralygodium meckertii Karafit et Stockey (2008)

Fertile pinnules

(Plate 4, Figs. 1-2)

Description: Abaxially enrolled lobed fertile pinnules (Plate 4, Fig. 1) are common at the Eden Main localities. Sporangia with apical annuli (Plate 4, Fig. 2). Spores trilete and smooth (Plate 4, Fig. 2). For a detailed description see chapter 3.

Occurrence: Over 50 specimens are known from the Eden Main localities. Figured specimen: P14457 E top.

Discussion: See chapter 3 where this taxon is described in detail.

Family: Cyatheaceae (*sensu* Kramer, 1990a)

Rachis with attached pinna

(Plate 4, Figs. 3-5)

Description: One specimen of a rachis and diverging pinna in transverse section is known (Plate 4, Fig. 3). The entire specimen is 1.3 cm long. The rachis and pinna are 5.5 mm and 3.5 mm wide respectively. The epidermis has been abraded on the entire specimen, leaving the hypodermis as the remaining outer layer. The hypodermis is sclerotic and *ca* nine cells thick, with cells up to 30 µm in diameter (Plate 4, Fig. 3).

Parenchyma cells in the ground tissue of the rachis are 36-68 µm in diameter. Mucilage cells are 42-96 µm in diameter in the ground tissue, occur singly or in groups of two, and occasionally have brown contents. Endodermis is unidentifiable. Each vascular strand is surrounded by a sclerotic sheath usually *ca* four cells thick but up to 15 cells thick on the inner side at concave areas of xylem corrugations (Plate 4, Fig. 4). Bundle sheath cells measure 24-60 µm in diameter.

There are two vascular bundles preserved in the rachis. The exact configuration of the bundles is unknown because part of the rachis has been abraded (Plate 4, Fig. 3). Gaps or crushed amorphous material on both sides of vascular bundles suggest bundles were amphiphloic (Plate 4, Figs. 4, 5). The xylem is composed of tracheids 1-2 cells wide that are circular to rectangular in transverse section. Metaxylem tracheids are 18-144 µm in diameter (Plate 4, Fig. 4). Xylem has a corrugated outline, individual corrugations are usually V- or sometimes U-shaped, with one protoxylem group in the former and two in the latter (Plate 4, Fig. 4). Xylem maturation is endarch, with protoxylem on the inner concave areas of each corrugation in the vascular strand (Plate 4,

Fig. 4). Individual protoxylem tracheids are 12-18 μm in diameter.

The histology of the attached pinna is similar to that of the rachis except that the stele is not as strongly corrugated (Plate 4, Fig. 5) and the sclerotic bundle sheath is not as well developed. The vascular bundle sheath of the pinna is similar to that of the rachis except that at concave areas of corrugation on the inner side of the xylem where it is only up to eight cells thick (Plate 4, Fig. 5).

The pinna vasculature consists of three bundles; the two adaxial bundles having roughly an inverted L-shape, while the abaxial bundle is roughly C-shaped (Plate 4, Fig. 5). The configuration of the xylem is of the *Cibotium*-type (Ogura, 1972). Metaxylem tracheids occur in 1-3 layers. There is one protoxylem group per corrugation that is often represented by a lacuna (Plate 4, Fig. 5).

Occurrence: Eden Main Ditch: P14504 B bot and C top.

Discussion: Rachides with corrugated vascular traces, three-parted pinna traces and secretory cells in the ground tissue are assignable to the Cyatheaceae *s.l.* (e.g., Nishida, 1984). Members of this family have an arborescent growth form and are often found in the tropics, often growing in the understory, in open environments or in montane or alpine habitats (Kramer, 1990a). The presence of a thick hypodermis in the fossil suggests that the rachis is from a mature plant, as juvenile members of the Cyatheaceae tend to lack a hypodermis (Nishida, 1984).

The anatomy of the rachis and pinna are comparable to many extant members of the "core group" of tree ferns in the Cyatheales (A. Smith et al., 2006). Rachides in several families of Cyatheales contain numerous free vascular bundles that are U-, V- or W-shaped that fuse at distal levels to form vascular strands like those seen in the fossil

specimen (Ogura, 1927a; Nishida, 1984). Vascular architecture similar to that of the fossil rachis can be found in Cyatheaceae, Dicksoniaceae, Cibotiaceae (*sensu* A. Smith et al., 2006) (Dicksoniaceae *sensu* Kramer 1990c), Metaxyaceae (Lucansky and White, 1974; Nishida, 1984), and Thyrsopteridaceae (*sensu* A. Smith et al., 2006) (Dicksoniaceae *sensu* Kramer, 1990c) (Nishida and Hara, 1979; Nishida, 1984). However, Cibotiaceae and Metaxaceae both lack mucilage cells in their ground tissues (Nishida, 1984). The three-parted pinna trace is more like that of *Cyathea* than that of other genera (Nishida, 1984, H. Nishida, personal communication, 2007).

Fossil taxa with comparable vascular architecture to the Eden Main tree fern include, *Cyathocaulis* Ogura (1927b), and *Cyathorachis* Ogura (1927b) (Nishida and Hara, 1979; Nishida, 1981, 1984). Both of these ferns have rachides with U- or V-shaped vascular bundles, that may fuse to form corrugated vascular strands like those seen in the Eden Main specimen (Nishida, 1984). *Cyathorachis* has a similar vascular arrangement to the Eden Main rachis, and some species have a thick hypodermis, but all known species lack mucilage cells in the ground tissue. *Cyathocaulis* is a genus of permineralized rhizomes with attached leaf bases from the Cretaceous of Japan (Ogura, 1927b; Hashimoto, 1971; Nishida, 1984). The leaf bases of *Cyathocaulis* have W- or U-shaped bundles that become V- or U-shaped distal to the rhizome. Leaf bases contain mucilage cells in the ground tissue (Nishida, 1984).

The Eden Main rachis is abraded making it difficult to determine the arrangement of all of the vascular tissues. Because of the complicated nature of the vascular architecture in this group, rhizome and/or better preserved rachis anatomy will be required to clarify the systematic affinities of the Eden Main tree fern.

Family: Dennstaedtiaceae *s.l.*

Isolated rachis type 1

(Plate 5, Figs. 1-2)

Description: An isolated fern rachis rachi from the Eden Main localities is 1.0 mm wide and 0.73 mm thick. The epidermis is abraded (Plate 5, Fig. 1). Ground tissue is composed of thick-walled parenchyma cells near the vascular tissue. The cells of the ground tissue measure up to 42 µm in diameter, and grade outward into sclerotic tissue with cells up to 21 µm in diameter (Plate 5, Fig. 1).

The vascular strand is U-shaped and one tracheid thick (Plate 5, Figs. 1, 2). Adaxial tips of the strand are hooked inward. Metaxylem cells are 15-30 µm in diameter and xylem maturation is endarch. Protoxylem tracheids measure 6-12 µm in diameter. There are two protoxylem strands, distinguished by their smaller size, on the abaxial arch of the trace, and probably one on the inner side of each adaxial hook (Plate 5, Fig. 2).

Occurrence: Exact Eden Main locality unknown, P14338 C top.

Discussion: The shape of the vascular strand in this rachis is similar to those seen in some members of the Dennstaedtiaceae *s.l.* (Ogura, 1972). Dennstaedtiaceae are currently found worldwide, mostly in warm climates, often growing in most understory or open environments (Kramer, 1990b). Molecular phylogenetic work has shown that Dennstaedtiaceae *sensu* Kramer (1990b) is polyphyletic (Hasebe et al., 1994, 1995) or paraphyletic (Wolf et al., 1994), however, if lindsaeoid ferns are treated as a separate family, the Dennstaedtiaceae is monophyletic (A. Smith et al., 2006; Schuettpelz and Pryer, 2007). Few dennstaedtiaceous fossils are known from the Late Cretaceous (Nishida, 1991; Serbet and Rothwell, 2003). Most of the fossil diversity for this group is

known from the Cenozoic, though even then, fossil records are rare (Collinson, 1996). Dennstaedtiaceae *s.l.* have the largest diversity of rachis anatomy (Keating, 1968) of extant ferns and it is assumed that the fossil record might contain a variety of anatomical forms assignable to the family.

Dennstaedtiaceous rachis type 2

(Plate 5, Fig. 3)

Description: Isolated dennstaedtiaceous rachis type 2 is 1.0-4.1 mm in diameter. The only specimens available are known from oblique transverse sections and preservation of the ground tissues is especially poor. One specimen, P13527 C bot, has an adaxial groove (Plate 5, Fig. 3). The ground tissue is poorly preserved, but appears to be parenchymatous. The epidermis is abraded, and there appears to be a poorly preserved sclerotic hypodermis outside of the ground tissue (Plate 5, Fig. 3).

The xylem is made up of one row of tracheids with scalariform secondary wall thickenings. The adaxial tips of the xylem are curved outward (Plate 5, Fig. 3). Phloem is not preserved (Plate 5, Fig. 3). The vascular trace is similar to the *Loxoma*-type (Ogura, 1972) being U-shaped (Plate 5, Fig. 3).

Occurrence: Eden Quarry; the Ditch: P13527 Cbot and P14320 G.

Discussion: The shape of the vascular bundle is similar to extant and extinct taxa assigned to the Dennstaedtiaceae *s.l.* (e.g., Arnold and Daugherty, 1964; Keating, 1968; Ogura, 1972, Nishida, 1991). A similar bundle is also seen in the genus, *Culcita* C. Presl in the Dicksoniaceae (*sensu* Kramer 1990c) (Keating, 1968; White and Turner, 1988).

Family: ?Blechnaceae/?Dryopteridaceae *s.l.*

Rachis

(Plate 5, Fig. 4)

Description: Isolated rachides are 3.5-4.1 mm in diameter, one specimen shows an adaxial groove (Plate 5, Fig. 4). Ground tissues are apparently parenchymatous, but are not well preserved.

Specimens are obliquely sectioned and the rachides are poorly preserved. At least three vascular bundles are present in each rachis, two on the adaxial and one or more on the abaxial side, each with a sclerotic bundle sheath (Plate 5, Fig. 4). Metaxylem tracheids are scalariform.

Occurrence: The Ditch; Eden Quarry: P13527 D bot d; P14345 F top.

Discussion: These specimens are not well preserved, but still display several vascular bundles with an arrangement similar to those seen in the *Aspidium*-type (Ogura, 1972). Ferns with an *Aspidium*-type rachis with, each vascular strand surrounded by a bundle sheath, are similar to some described fossils of the Blechnaceae e.g., *Woodwardia virginica* Pigg et Rothwell (2001), or *Trawetsia princetonensis* Smith, Stockey, Nishida et Rothwell (2006). Many members of extant Blechnaceae and some Dryopteridaceae also have a *Aspidium*-type rachis, with numerous vascular bundles, but Blechnaceae often has thick bundle sheaths (Ogura, 1972). Cretaceous records of the Blechnaceae or Dryopteridaceae are rare (Tidwell and Ash, 1994; Skog, 2001), but fossils become common during the Cenozoic (Collinson, 1996).

Family: ?Dryopteridaceae *s.l.*

Rachis

(Plate 5, Fig. 5)

Description: An isolated rachis 3.0 mm in diameter is known from the Eden Main localities. This rachis is abraded with epidermis and most of the hypodermis removed. Where present, the hypodermis consists of *ca* six layers of thick-walled cells 18-42 μm in diameter. The ground tissue is composed of parenchymatous cells that are 72-84 μm in diameter (Plate 5, Fig. 5). Vascular bundles are hippocampiform (seahorse-shaped) with infolded adaxial hooks. Metaxylem tracheids are scalariform, 30-72 μm in diameter, and protoxylem is unknown (Plate 5, Fig. 5).

Occurrence: The Ditch: P14511 A2, and B top.

Discussion: The vascular arrangement in this rachis is similar to Ogura's (1972) *Onoclea*- type, found in the Dryopteridaceae *s.l.* (Ogura, 1972). This family has worldwide distribution (Tryon and Tryon, 1982; Kramer et al., 1990), and appears to be polyphyletic (Hasebe et al., 1994, 1995), or paraphyletic (A. Smith et al., 2006; Schuettpelz and Pryer, 2007). Recently, evidence has been given that removal of three genera, *Didymochlaena, Hypodematium*, and *Leucostegia* may render the family monophyletic (A. Smith et al., 2006; Schuettpelz, 2007; Schuettpelz and Pryer, 2007). The Dryopteridaceae, or a closely related group, extend into the Early Cretaceous. This is supported by fossil (e.g., Deng, 1994, 1995; see Skog, 2001 for review) and molecular dating evidence (Schneider et al., 2004). Most of the Cretaceous record of the family is known from compression/impression fossils (see Skog, 2001). The only Mesozoic permineralized specimen of probable dryopteridaceous affinity is known from the Late

Cretaceous (Campanian) of Alberta, Canada, but this specimen could also belong to the Blechnaceae (Serbet and Rothwell, 2006). Only the discovery of reproductive structures will allow for the confident placement of the Eden Main rachides into Dryopteridaceae.

Family: Incertae sedis

Unidentified rachis

(Plate 5, Figs. 6-7)

Description: Two isolated rachides are 0.8-2.3 mm in diameter. The ground tissue is parenchymatous becoming sclerotic towards the periphery of the rachis (Plate 5, Fig. 6). The epidermis is missing. The first layer of ground tissue out side the stele is parenchymatous (Plate 5, Fig. 7), the next 1-2 layers of ground tissue are composed of thick-walled cells with simple pits (Plate 5, Fig. 7). The rachides have two C-shaped vascular bundles that are oriented with their concave sides facing one another, and attached to the ground tissue on their concave sides by a "bridge" of thick-walled cells (Plate 5, Fig. 6). Tracheids have scalariform secondary wall thickenings. A gap between the xylem and ground tissue represents the previous location of the phloem.

Occurrence: Eden Quarry: P14454 G top; P14471 A.

Discussion: This rachis has a unique vascular architecture when compared to known fossil and extant fern frond segments. Since vascular architecture in fern fronds is quite diverse (e.g., Ogura, 1972), and bundle arrangement can change in individual ferns depending on the level of section, this specimen will most likely remain unclassified until attached rhizomes or different levels of section can be examined.

Exarch solenostelic fern rhizome *cf. Solenostelopteris*

(Plate 6, Figs. 1-6)

Description: Two solenostelic rhizomes with similar anatomy are 1.3-2.2 mm in diameter. Oblique transverse sections of the rhizomes show departing rachis and root traces (Plate 6, Figs. 1, 4, 5, 6).

The entire cortex is up to 0.5 mm thick (Plate 6, Figs. 1, 2, 4, 5, 6) and composed of tightly packed parenchyma cells. The inner cortex is up to 0.4 mm thick made up of thin-walled cells up to 70 μm in diameter (Plate 6, Figs. 1, 2, 4). The middle cortex is composed of thick-walled cells, sometimes with dark contents, up to 60 μm in diameter (Plate 6, Figs. 1, 2, 4). One rhizome displays an abraded outer cortex that is missing completely from the other specimen (Plate 6, Fig. 2). The outer cortex is composed of thin-walled cells up to 40 μm in diameter. This zone is difficult to interpret as it is abraded and not well preserved (Plate 6, Fig. 2).

Pericycle and phloem are not preserved (Plate 6, Figs. 1, 3, 4). Metaxylem tracheids are 18-54 μm in diameter, with scalariform secondary wall thickenings. Xylem is 1-3 tracheids thick. Xylem parenchyma is not present/preserved. Xylem maturation is exarch. The first formed metaxylem tracheids have scalariform secondary wall thickenings and are found in groups scattered around the stele (Plate 6, Fig. 3). Up to two leaves have been observed departing from a rhizome simultaneously (Plate 6, Fig. 4). The endodermis is one cell layer thick, with cells up to 12 μm in diameter (Plate 6, Figs. 1, 3, 4, 5). The pith is 0.3-0.4 mm in diameter and is composed of thin-walled, tightly-packed parenchyma cells *ca* 70 μm in diameter (Plate 6, Figs. 1, 3, 4, 5).

Leaf trace departure suggests that the rhizome had dorsi-ventral symmetry. Three

leaf traces have been observed in one of the rhizomes. The first leaf departed from one side of the rhizome. About 2.5 mm distal to this leaf, a second leaf trace departed from the same side of the rhizome as the first. At the same level of section as the second trace, another trace was observed in oblique section, departing from nearly the opposite side of the rhizome (Plate 6, Fig. 4). Parenchyma from the pith and endodermis accompanies each leaf trace as it extends through the cortex (Plate 6, Figs. 4, 5). Leaf gaps formed by the departure of leaf traces are open for *ca* 90 peels (ca 2.3 mm). The leaf trace is C-shaped and one to two tracheids thick, with endarch xylem maturation (Plate 6, Figs. 4, 5). Phloem of the trace is not preserved.

Root traces have only been observed departing from one side of the rhizome, *ca* 90° to leaf traces. Diverging root traces do not seem to be associated with leaf trace divergence (Plate 6, Fig. 1). Root traces are *ca* 0.3 mm wide, diarch (Plate 6, Fig. 6), have preserved thick-walled parenchymatous ground tissue and poorly preserved vascular tissues.

Occurrence: Eden Quarry; Eden Main Ditch: P14489 B bot, C top; P14492 C bot and D.

Discussion: A few fern families (e.g., Loxomataceae and Schizaeaceae) (Boodle, 1901, Seward and Dale, 1901) have an exarch solenostele similar to those found in the fossil rhizomes. Classification of ferns based solely on rhizome anatomy is generally difficult. Until more and better preserved specimens can be found, comparison to extant ferns will not be possible.

Fossil rhizomes with an exarch solenostele are assigned to the morphogenus *Loxsomopteris* Skog (1976) or *Solenostelopteris* Kershaw (1910). The distinguishing factor between these two taxa is the presence of multicellular trichomes in *Loxsomopteris*

(Skog, 1976; Nishida and Nishida, 1982). Because of the abraded surface of the Eden Main rhizome, the presence or absence of trichomes cannot be confirmed.

The Eden Main rhizome is comparable to several described species of *Solenostelopteris* or *Loxsomopteris,* but there are distinguishing characters (Table 2). *Loxsomopteris* rhizomes have been compared to extant *Loxsomopsis* (Skog, 1976; Nishida and Nisida, 1982). The affinities of *Solenostelopteris* are unclear and the various species may not be closely related (Bohra and Sharma, 1979; Little et al., 2006b). *Solenostelopteris japonica* Kershaw (1910), *Solenostelopteris leithii* Tidwell et Skog (1999), *S. medlynii* Tidwell et Skog (1999) all have a zonated pith, unlike the homogenous pith found in the Eden Main rhizome (Table 2). *Solenostelopteris nipanica* Vishnu-Mittre (1958), *Loxsomopteris loxsomoides* (Ogura) M. Nishida et H. Nishida (1982) and *L. anasilla* Skog (1976) have a sclerotic pith, unlike the parenchymatous pith of the Eden Main rhizome. *Solenostelopteris skogiae* Little, Stockey et Rothwell (2006b) and *S. jurassica* Bohra et Sharma (1979) both lack xylem parenchyma, have a parenchymatous pith, a stele that can be less then 1.0 mm in diameter, and grouped protoxylem like the Eden Main rhizome (Table 2). *Solenostelopteris skogiae* lacks a zoned cortex unlike the Eden Main rhizome (Little et al., 2000b). *Solenostelopteris jurassica* has an inner cortex of mixed parenchyma and sclerenchyma, a sclerotic outer cortex, and is covered in uniseriate multicellular trichomes (Bohra and Sharma, 1979). While the Eden Main fossil has a parenchymatous inner cortex, a thick-walled middle cortex and what appears to be a parenchymatous outer cortex that is mostly abraded. No evidence of trichomes have been found. The Eden Main fossil may, therefore, differ enough from other described species of *Solenostelopteris* to deserve designation as a

new species.

Table 2. Comparison of *Solenostelopteris* and *Loxsomopteris* species.

		Eden Main Rhizome	*S. skogiae* Little et Stockey	*S. japonica* Kershaw	*S. nipanica* Vishnu-Mittre	*S. sahni* Vishnu-Mittre	*S. jurassica* Bohra et Sharma	*S. leithii* Tidwell et Skog	*S. medlynii* Tidwell et Skog	*L. loxsomoides* (Ogura) Nishida et Nishida	*L. anasilla* Skog
Rhizome	Diam. (mm)	1.3-2.2	1.3-1.6	2.2 +	ca. 2	2-8	1.1-4.6	10+	8+	4-7	5
Pith	Zonation	No	No	Yes	No	No	No	Yes	Yes	No	No
	Inner-	Parenchymatous	Parenchymatous (similar to cortex)	Sclerotic (large cells)	Sclerotic	?/Parenchymatous	Parenchymatous (smaller than cortex)	Parenchymatous	Parenchymatous (large cells)	Sclerotic	Sclerotic
	Outer-	Parenchymatous	N/A	Sclerotic (small cells)	Sclerotic	?/Parenchymatous	Parenchymatous (smaller than cortex)	Sclerotic	Parenchymatous (small cells)	Sclerotic	Sclerotic
Stele	(Diam; mm)	0.5-0.7	0.5	1.8	1-1.3	1-2	0.8-1.6	2.6-5.8	4.6-5.5	2.8-4.8	2.3
	PX- 1st formed tracheids	No grouped	No grouped	No grouped	? grouped & scattered	? scattered	?Yes grouped	No ? scattered	? ?	No scattered	No ? scattered
	Xylem parenchyma	No	No	Yes	Yes	Yes	No	Yes*	?	Yes	? Yes
Cortex	Zonation	Yes	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Epidermis	Trichomes	?	absent	?	?	?	Uniseriate multicellular	?	?	Conical	Bristle-like
Age		Late Cretaceous	Early Cretaceous	Late Cretaceous	Early Cretaceous	Early Cretaceous	Early Cretaceous	Late Jurassic	Late Jurassic	Late Cretaceous	Early Cretaceous
Geographic	Distribution	Canada	Canada	Japan	India	India	India	USA	USA	Japan	USA

(Modified from Little et al., 2006b Tidwell and Skog 1999; additional data from Ogura 1930; Bohra and Sharma 1979; Banerji 2000.)

* as interpreted from plate

Unidentified solenostelic rhizome with three-bundled leaf trace

(Plate 7, Figs. 1-5)

Description: A single amphiphloic, siphonostelic rhizome has been identified with leaf traces consisting of three vascular bundles. The rhizome is 2 mm in diameter and at least 1 cm long. Transverse sections of the rhizome show well-preserved ground and vascular tissues (Plate 7, Figs. 1-3, 5). The rhizome has dorsi-ventral symmetry, and departing leaves, and roots have been abraded from the outside of the cortex.

The pith is *ca* 0.4 mm in diameter and is composed of two zones. In the inner sclerotic zone cells up to 30 μm in diameter, have thick walls and small lumina (Plate 7, Figs. 1, 2). The outer zone of pith is up to 54 μm thick and composed of thin-walled cells 24 μm in diameter (Plate 7, Fig. 2).

Tracheids, phloem and parenchyma of the stele are preserved. The inner and outer endodermis are composed of cells, rectangular in cross section, up to 21 μm in diameter (Plate 7, Figs. 1, 2, 3, 5). The pericycle is composed of parenchymatous cells 12-30 μm in diameter (Plate 7, Figs. 2, 5). Phloem composed of thin-walled cells, 9-15 μm in diameter, many of which are crushed, lies between the pericycle and the conjunctive parenchyma (Plate 7, Fig. 2). Between the phloem and xylem is a layer of conjunctive parenchyma that ensheaths the xylem and is composed of cells similar to those in the pericycle (Plate 7, Fig. 2.). The entire zone of thin-walled cells between the endodermis and xylem can be up to 75 μm thick. Xylem is 2-4 tracheids thick, and up to 90 μm wide. Tracheids are 12-33 μm in diameter (Plate 7, Figs. 1, 2, 3, 5). Interspersed with the tracheids are xylem parenchyma cells, up to 18 μm in diameter (Plate 10, Fig. 2). The stele gives rise to two leaf traces and several adventitious roots along the roughly

400 peels (10 mm) made of the rhizome.

The cortex has three distinct layers (Plate 7, Fig. 1). The innermost layer is parenchymatous up to 120 μm thick with cells up to 30 μm in diameter (Plate 7, Figs. 1, 2, 3, 5). This layer resembles the outer layer of the pith. The middle cortex is up to 0.2 mm thick composed of sclerenchyma cells up to 54 μm in diameter, with thick walls and small cell lumina (Plate 7, Figs. 1, 2, 3, 5). This layer resembles the tissue of the center of the pith. The outer cortex is abraded, 0.3 mm thick and composed of thick-walled parenchyma cells, up to 54 μm in diameter (Plate 7, Figs 1, 3, 4).

Two leaf traces depart from opposite sides of the rhizome. In transverse section, leaf trace formation is first noticeable when the pith and a portion of the stele extend laterally. A C-shaped bulge in the stele then divides forming two asymmetrical reniform bundles (Plate 7, Fig. 3). The abaxial end of the largest bundle eventually separates forming a small, round abaxial bundle. The leaf trace contains three bundles as it proceeds through the cortex and into the leaf base. Leaf gaps are open for at least 2.8 mm. The ground tissues in the leaf are not well preserved, but appear to be similar to those in the rhizome (Plate 7, Fig. 4).

Root traces are all produced on one side of the stele, while the leaves arise on the other side, suggesting that the rhizome had dorsi-ventral symmetry. Root traces are poorly preserved (Plate 7, Figs. 1, 5), and are broken off outside of the cortex.

Occurrence: Eden Quarry: P14579 B bot and C top.

Discussion: Filicalean fern rhizomes with leaf traces with three or more vascular bundles, are usually dictyostelic (e.g., Ogura, 1972). Solenostelic rhizomes with three bundled leaf traces are almost unknown in extant, or fossilized fern rhizomes (G.W.

Rothwell, personal communication, 2006).

Ferns in the Grammitidaceae have solenostelic rhizomes and usually have a V-shaped *Grammitis*-type leaf trace (Ogura, 1972). There are, however, two extant species in the Grammitidaceae that are comparable to the Eden Main rhizome: *Zygophlebia goodmani* Rakotondrainibe et Deroin (2006) and *Z. anjanaharibensis* Rakotondrainibe et Deroin (2006) from Madagascar. In cross section they often appear to have a leaf trace with one abaxial and two adaxial bundles similar to that of the Eden Main fern (Rakotondrainibe and Deroin, 2006). However, the abaxial bundle in *Zygophlebia goodmani* and *Z. anjanaharibensis* is actually a bud trace, formed by the union of two vascular strands (Rakotondrainibe and Deroin, 2006). The adaxial traces arise independently from the sides of the leaf gap (Rakotondrainibe and Deroin, 2006). The leaf trace of the Eden Main fern is superficially similar to that of *Zygophlebia goodmani* and *Z. anjanaharibensis* but the entire trace of the Eden Main rhizome departs as an arch, that divides into three bundles, all of which appear to enter the leaf. Most species of *Zygophlebia* have breaks in the stele that are not associated with leaf trace departure (Bishop, 1989; Rakotondrainibe and Deroin, 2006), a feature not seen in the Eden Main fossil. The zoned ground tissues of *Zygophlebia goodmanii* and *Z. anjanaharibensis* (Fig. 3 A-F in Rakotondrainibe and Deroin, 2006) are similar to the ground tissues of the Eden Main specimen, but this is probably not a good indication of phylogenetic affinity.

It is difficult to say if the Eden Main rhizome shows affinities with the Grammitidaceae because little work has been done on the anatomy of the family (Parris, 1990). Fossil records of the family (Gómez,1982), or fossils that have been recognized as having a possible affinity to the family (Little et al., 2006a) are rare.

Conclusions: Fern fossils found at the Eden Main localities reveal that taxa from both the second and the third evolutionary radiation of filicalean ferns (Lovis, 1977; Rothwell, 1987) were present in western North America during the Coniacian. Organs of Gleicheniaceae are commonly found, while organs of other members of the second radiation (e.g., Schizaeaceae and Cyatheaceae) are less common. Some rachides are known that may be assignable to families that originated during the third radiation, but they are not common. Some frond segments may be the oldest record of the Blechnaceae and others may represent the first permineralized Dryopteridaceae. Geographic localities with similar fern assemblages today may be found in the tropics, e.g., South America and New Zealand (e.g., Kramer, 1990a, 1990b, 1990d; Kramer et al., 1990).

Chapter 3*

Eden Main Flora: *Paralygodium meckertii*

Family: Schizaeacae

Genus: *Paralygodium* Yoshida, H. Nishida et M. Nishida

Paralygodium meckertii Karafit et Stockey

(Plate 8, Figs. 1-7; Plate 9, Figs. 1-6; Plate 10, Figs. 1-6; Plate 11, Figs. 1-4)

Filicalean ferns of the family Schizaeaceae Kaulf. currently occur mostly in the tropics of the Southern Hemisphere (Kramer, 1990). Traditionally this family contained four genera; *Lygodium* Sw., *Anemia* Sw., *Mohria* Sw. and *Schizaea* J.E. Smith, all of which have sculptured spores, apical or sub-apical annuli (Kramer, 1990), and croziers that are enrolled with their adaxial surfaces exposed (Rothwell, 1999). The species traditionally included in the genus *Mohria* are now considered as part of the genus *Anemia* (Mickel, 1962, Skog et al., 2002; Wikström et al., 2002; Smith et al., 2006). Some authors, however, additionally recognize the genus *Actinostachys* Wallich as separate from *Schizaea* (e.g., Skog et al., 2002, Smith et al., 2006). Recently, Smith et al. (2006) suggested that these genera comprise a clade of three families, Order Schizaeales, that is sister to the core leptosporangiate ferns.

The fossil record for Schizaeaceae extends back at least to the Jurassic (Cleal, 1993) and perhaps the Triassic (Tidwell and Ash, 1994, Skog, 2001, Axsmith, 2007). Some Mesozoic and Cenozoic schizaeaceous fossils with sporangia and spores are known but many are poorly understood due to their preservation as compression/impressions.

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Fossils of the family are centered in the Northern Hemisphere (Kvaček et al., 2006).

Anatomically preserved specimens, though less common, yield more informative characters than compression/impressions, as they include internal anatomy as well as external morphology. Permineralized schizaeaceous remains include: *Schizaeangium* Bohra et Sharma (1978), pinnule tissue with sporangia and spores from the Jurassic of India; *Schizaeopteris* Stopes et Fujii (1910), fertile pinnules from the Cretaceous of Japan (Yoshida et al., 1996); *Anemia quatsinoensis* Hernandez-Castillo, Stockey et Rothwell (2006), well-preserved fertile pinnae with sporangia and spores (Lower Cretaceous of North America), and *Anemia poolensis* Chandler (1955) from the Paleocene/Eocene of England, known from external morphology and spores. The most widespread genus, *Paralygodium* Yoshida, Nishida et Nishida (1997), was described based on permineralized schizaeaceous pinnules, known from the Cretaceous of Japan as well as the Eocene of North America (Trivett et al., 2006).

Specific diagnosis: Pinnules pinnately lobed, 1.6-3.0 mm wide, 2.1-3.6 mm long, abaxially enrolled. Major lobes three, each with 3-4 minor lobes; minor lobes abaxially enrolled, imbricate. Sporangia abaxial in two rows, exindusiate, pyriform, 360-468 μm long, 216-300 μm wide, attached basi-laterally by short, broad stalk. Annulus apical, 15-18 cells. Spores trilete, tetrahedral-globose, with round to triangular amb, 33-42 μm in diameter; equatorial flange absent; laesurae extending seven-eighths distance to equator; exine psilate.

Holotype: P14457 E top, University of Alberta Paleobotanical Collections (UAPC-ALTA).

Description: *Paralygodium meckertii* specimens are found as isolated enrolled pinnules, 1.6-3.0 mm wide and 2.1-3.6 mm long (Plate 8, Figs. 1-5). Pinnules bear three major lobes each of which divide distally into 3-4 minor lobes (Plate 8, Figs. 1-2). Each pinnule has a winged base in transverse section suggesting that the frond was pinnatifid (Plate 8, Fig. 1; Plate 9, Fig. 3). Abaxial and adaxial epidermal cells are rectangular with sinuous outlines (Plate 8, Fig. 6), and the abaxial epidermis bears circular stomata up to 36 µm in diameter (Plate 8, Fig. 7). A single vascular bundle enters the base and distally branches into each minor pinnule lobe (Plate 8, Fig. 4). Three dimensionally reconstructed Pinnule morphology shows a pinnate organization (Plate 11, Figs. 1-4). Lobes are circinately coiled with abaxial sporangia located in the resulting subspheroidal spaces (Plate 8, Figs. 2, 3, 5; Plate 9, Fig. 2; Plate 11, Figs. 1-4).

The three major pinnule lobes are 0.9-2.1 mm wide, the minor lobes are up to 0.85 mm wide (Plate 8, Figs. 1, 2; Plate 9, Fig. 1). The terminal major lobe may divide into 3-4 minor lobes while the lateral major lobes have only been observed with three minor lobes (Plate 8, Fig. 2). Each lobe contains an inflated midrib that bears a single terete vascular strand (Plate 8, Figs. 2, 3; Plate 9, Fig. 2) that extends nearly to the tip.

Minor lobes imbricate with neighboring lobes proximally and are free distally. Axially elongate cells of the midrib region are 12 µm in diameter and often contain brown contents (Plate 8, Figs. 3, 4; Plate 9, Figs. 1, 2, 3, 6). In longitudinal section vascular bundles show tracheids with scalariform secondary wall thickenings (Plate 9, Fig.4). The midrib of each minor lobe is inflated with sporangia attached on either side. An adaxial ridge of thick-walled cells, up to 66 µm wide and 132 µm long occurs as a layer 2-3 cells thick in the center of each pinnule lobe tapering to a single layer laterally

(Plate 8, Figs. 1, 3, 4). Sporangia are attached in two rows on the abaxial side of pinnule lobes, and occur among numerous trichomes or paraphyses that are often seen flattened between the rows (Plate 9, Fig. 5). Sporangia are pyriform, 360-468 µm long and 216-300 µm wide, with an apical uniseriate annulus (Plate 9, Fig. 6). Longitudinal sections of the sporangia reveal that they are basi-laterally attached to pinnule midribs by a short, broad stalk (Plate 9, Fig. 6). The annulus is apical and consists of a uniseriate ring of 15-18 cells (Plate 9, Figs. 5, 6). Many sporangia appear to be senescent, having shed their spores, but several still contain spores. There are 105 to 159 spores in any one sporangium, making the spore count 128-256/sporangium.

Spores are psilate with no obvious perispore, trilete and tetrahedral to tetrahedral-globose, and 33-42 µm in diameter (Plate 10, Figs. 1-5). The laesurae extend seven-eighths the distance to the equator (Plate 10, Figs. 1, 2). Broken spores under SEM reveal a dense exospore (Plate 10, Figs. 5, 6). Numerous small holes, ≤1.0 µm in diameter, occur in the exospore on all faces of spores including the trilete suture (Plate 10, Figs., 3, 4, 6), and may be caused by taphonomic or fungal damage. Spores correspond to the sporae dispersae genus *Deltoidospora* Miner (Miner, 1935; A.R. Sweet personal communication, 2007).

Occurrence: Eden Main Quarry; the Ditch; Eden 400; Eden Creek; Eden Main 2nd Ditch. Figured Specimens: P14320 E bot; P14457 E top; P14468 B top, C bot, and D.

Discussion: The Eden Main fossil fern has pinnules bearing abaxial pyriform sporangia with short stalks and a uniseriate apical annulus. These characters are diagnostic for Schizaeaceae (Eames, 1936; Kramer, 1990d). Abaxially enrolled pinnules are also diagnostic for the family (Rothwell, 1999).

Of the extant Schizaeaceae, only the genus *Anemia* Sw., like the Eden Main fossils, has exindusiate sporangia borne on skeletonized pinnules (Kramer, 1990d). Pinnule morphology and spores of fossils similar to the Eden Main fossil (Table 3) have been compared to species in extant *Anemia,* Subgenus *Coptophyllum* (Chandler, 1955; Mickel, 1962; Trivett et al. 2006). Species in this subgenus have pinnules that may remain enrolled through maturity (Chandler, 1955; Collinson, 2001), and 128-256 spores per sporangium (Mickel, 1962; J.T. Mickel, personal communication, 2006). All known mature spores of extant *Anemia* are highly sculptured, although some species have smooth spores when they are immature (van Konijnenburg-van Cittert, 1991; Dettmann and Clifford, 1992). Mickel (1962) also noted that the perine layer of *A. gardneri* Brade is easily removed, leaving the exine with a nearly smooth appearance. Because many sporangia in the Eden Main fossils seem to have already shed their spores, and remnants of perispore are not seen on in situ spores, it would appear that they were psilate at maturity.

The abaxial and adaxial epidermal cells on the fossil pinnules are thick-walled with sinuous margins and similar to those reported in *A. tomentosa* var. *mexicana* Presel or *A. gardneri* (Mickel, 1962). It is difficult to determine the position of stomata in relation to subsidiary cells on the fossil specimens. In *Anemia* Subgenus *Coptophyllum*, the most common stomatal arrangement is polocytic (Leaf Architecture Working Group, 1999), also known as "applied" stomata (Mickel, 1962, Mickel and Lersten, 1967). In plants with this arrangement, each stoma is located at the distal end of a subsidiary cell and almost entirely surrounded by it. In some species of subgenera *Coptophyllum* and *Anemiorrhiza,* desmocytic (Leaf Architecture Working Group, 1999), or "suspended"

stomata (Mickel, 1962, Mickel and Lersten, 1967) are found, where a subsidiary cell surrounds the stoma and one anticlinal wall cuts into the cell (Leaf Architecture Working Group, 1999). In a few species in subgenus *Coptophyllum*, and in more derived subgenera, stomata occur in the center of an epidermal cell without contacting its walls, a condition known as amphipericytic (Leaf Architecture Working Group, 1999), e.g., "floating stomata" or "adetostomy" (Mickel, 1962; Mickel and Lersten, 1967).

Schizaeaceous taxa have been described with fertile pinnules that are abaxially enrolled to some degree from both compression/impression and permineralized remains as old as the Jurassic or possibly the Triassic (Tidwell and Ash, 1994; Skog, 2001; Axsmith, 2007). Some of these include: *Schizaeopteris mesozoica* Stopes et Fujii (Stopes and Fujii 1910, Yoshida et al., 1996); *Anemia fremontii* (Knowlton) forma *fertilis* Andrews (Andrews and Pearsall, 1941; Collinson, 2001); *Anemia sphenopteroides* (Fontaine) Skog (1992), *Anemia dicksonioides* (Fontaine) Skog (which includes *Pelletixia amelguita* Skog; *sensu* Skog 1992); *Klukiopsis jurassica* Deng et Wang (2000); and *Anemia quatsinoensis* Hernandez-Castillo, Stockey et Rothwell (2006). Of these taxa, all but *Klukiopsis* bear sculptured spores. *Klukiopsis* is a compression/impression fossil from the Jurassic of China that contains smooth, trilete spores that are similar in size to those of the Eden Main fossils. But there are over 800 spores reported per sporangium in *Klukiopsis* vs. 128-256 in the Eden Main specimens.

Anatomically preserved schizaeaceous ferns with enrolled, seemingly mature fertile pinnules bearing psilate, trilete spores have been placed either in the genus *Anemia* (Chandler, 1955) or *Paralygodium* Yoshida, H. Nishida et M. Nishida (Yoshida et al., 1997, Trivett et al. 2006). *Anemia poolensis* is known from the Eocene and Paleocene-

Eocene boundary of England (Chandler 1955, 1961, 1962, 1963; reviewed by Collinson, 2001) the enrolled pinnule, and smooth spores (Table 3) are similar to the Eden Main fossils and previously described species of *Paralygodium* (Yoshida et al. 1997; Trivett et al. 2006). However, *A. poolensis* is carbonized and partially pyritized (Chandler, 1961) preserving the external morphology, but the pinnule histology is poorly preserved, making comparisons to *Paralygodium* difficult. Therefore, *Anemia poolensis* has typically been treated in a separate taxon (Yoshida et al., 1997, Trivett et al., 2006). Perhaps with additional, better preserved specimens of *A. poolensis*, the relationships between these taxa could be clarified.

Paralygodium yezoense Yoshida, H. Nishida et M. Nishida (1997) from the Late Cretaceous (Turonian-Santonian) of Japan, has enrolled palmate pinnules that form a globose structure in which sporangia are attached. Similar pinnule architecture is found in *P. vancouverensis* Trivett, Stockey, Rothwell et Beard (2006) from the Eocene of Vancouver Island. Both of these taxa have similar anatomy, but vary in arrangement of pinnules on the pinna, number of pinnule lobes, pinnule size, and spore structure (Table 1), while the Eden Main fossil ferns share characters with both species of *Paralygodium*; they have a distinct pinnule architecture. Individual pinnules are pinnately lobed with three proximal lobes and *ca* 10 lobes distally. All of these lobes are enrolled abaxially forming three subspheroidal spaces on each pinnule. *Paralygodium vancouverensis* and *P. yezoense* both have palmate pinnules that enroll forming a subspheroidal structure in which sporangia occur. *Paralygodium vancouverensis* has *ca* seven lobes (Trivett et al. 2006) and *P. yezoense* has 9-13 lobes (Yoshida et al. 1997) (Table 3).

Spores of all species of *Paralygodium* as well as those of *Anemia poolensis* are trilete, psilate, and tetrahedral to tetrahedral-globose. The spores of *Paralygodium yezoense* have an equatorial flange that surrounds each spore (Yoshida et al. 1997). This flange is lacking in *P. vancouverensis*, the Eden Main fossils and *Anemia poolensis* (Table 3). The Eden Main fossils have 128-256 spores per sporangium while the other species that have enough spores to be counted, are interpreted as having 128 per sporangium. This variation can be seen in living species of *Anemia*, some of which are known to have either 128 or 256 spores per sporangium on the same pinnule (Mickel, 1962; J.T. Mickel personal communication 2006). The size of sporangia and spores are generally consistent with the other species described above (Table 3).

The cause of the small holes in the exine of *P. meckertii* spores is unknown, but could be due to fungal damage or taphonomic causes. Elsik (1966) noted 0.25- 2 μm diameter perforations on Mississippian, Early Cretaceous and Tertiary spores and pollen that he attributed to chytrid damage. However, Elsik (1966) only figured light microscope images of these perforations. The presence of perforations on all faces of the Eden Main fossil spores including the area of the trilete suture suggest that they are spore damage of some type.

Because of the unique pinnule architecture in the Eden Main fossil fern, pinnate vs. palmate pinnule lobes, larger number of spores per sporangium, and spores lacking equatorial flanges (*Deltoidospora*), I have described it as a new species of the genus *Paralygodium*; *P. meckertii*. This new species adds to our knowledge of extinct diversity as well as morphological variation within the Schizaeaceae. *Paralygodium* is now known to have occurred on both sides of the Pacific Ocean during the Late Cretaceous,

having species in both Japan and western North America. The presence of this genus at the Appian Way locality on Vancouver Island suggests that *Paralygodium* remained in North America until at least the Eocene.

Table 3. Comparison of morphology, spores and age of fertile pinnules of Paralygodium spp. and Anemia poolensis.

Taxa	Paralygodium yezoense	P. meckertii	*P. vancouverensis*	*Anemia poolensis*
Pinnule Attachment	Alternate, Pinnate	?	Clusters of 3	Clusters
Pinnule Width	1.5-2.0 mm	1.6-3.0 mm	2.2-3.0 mm	2.0-3.0 mm
Pinnule Lobes	Palmate	Pinnate	Palmate	? Palmate
# Lobes	9-13	9-10	~7	4-≥7
Paraphyses	+	+	+	+
	2 rows alt	2 rows	2 rows	2 rows
Sprg1 Arrangement	~Sessile, Basi-lateral	Short Stalked, Basi-lateral	Short Stalked, ~Basi-lateral	Short Stalked-Sessile
Sprg Length	280-350 µm	360-468 µm	420-600 µm	250-440 µm
Sprg Width	190-240 µm	216-300 µm	275-325 µm	200-300 µm
Annulus	15-24 Cells	15-18 Cells	14-18 Cells	~15 Cells
Spores	33-40 µm	33-42 µm	30-48 µm	40-60 µm
Equatorial Flange	+	-	-	-
Age	Turonian-Coniacian	Coniacian	Eocene	Paleocene-Eocene

(Data from Chandler, 1955; Yoshida et al., 1997; Collinson, 2001; Trivett et al.,2006)

1 Sporangial

Chapter 4

Eden Main Flora: Seed plants

Introduction: The remains of gymnosperms and angiosperms are common in concretions found at the Eden Main fossil localities. Conifer remains include a stem of an extinct cycadeoid, and several vegetative and reproductive conifer organs. The most common identifiable fossil plant organ at all of the localities are leaves of Cupressaceae. Angiosperm fossils are not as common as the Cupressaceae, but they are more diverse and include representatives of the Lauraceae, Platanaceae, Nyssaceae, and a possible member of the Ericales. Several angiosperm taxa are known which can not currently be placed in extant or extinct families. Many seed plant families present at Eden Main have extant representatives with the bulk of their extant members living in the tropics in the Southern Hemisphere (e.g., Araucariaceae, Lauraceae), while others (e.g., Pinaceae) are found mostly in the Northern Hemisphere (Stevens, 2001 onwards).

Subdivision: Cycadeoidophytina

Cycadeoid with resin canals in the cortex and a woody eustele

(Plate 12, Figs. 1-4)

Description: A seed plant stem 3.5 cm long and 3.6 cm wide (Plate 12, Figs. 1-4) is known from the Eden Main localities. The pith is parenchymatous (Plate 12, Fig. 3) and surrounded by the stele. The eustele is 6 mm in diameter, and contains secondary tissues (Jud et al., 2008) (Plate 12, Fig. 2). The cortex is 9 mm thick, and contains numerous elongate, branched mucilage ducts (Plate 12, Figs. 2-4).

Numerous leaf and adventitious root traces have been observed departing from the stele (Jud et al., 2008). Leaf traces are composed of 1-8 vascular bundles arranged in

tangentially elongate rows (Jud et al., 2008) (Plate 12, Fig. 3). All of the observed root traces are non-girdling (Jud et al., 2008). Evidence of herbivory exists in this stem including a large gallery in the pith with a 3.0 mm wide entrance/exit wound (Jud et al., 2008) (Plate 12, Fig. 4). This gallery is lined with wound response tissue that may be comparable what has been called "nutritive tissue" in galls (e.g., Stone and Schönrogge, 2003; Jud et al., 2008) (Plate 12, Fig. 4). Numerous small galleries containing oribatid mite coprolites are found in the cortex (Jud et al., 2008).

Occurrence: Eden Quarry: P14371 A and B.

Discussion: The presence of a woody eustele with a wide cortex, branching mucilage ducts and non-girdling leaf traces allow for the identification of this stem as a cycadeoid. Cycadeoid anatomy is somewhat similar to that of extant and fossil cycads. However, the leaf traces of cycadeoids do not girdle the stem (Stewart and Rothwell, 1993). The preservation of insect damage and wound response in this plant provides information on Late Cretaceous plant/animal interactions. This fossil is currently being studied by Nathan Jud at Ohio University.

Subdivision: Coniferophytina

Family: Pinaceae

Five-needle pine leaves

(Plate 13, Figs. 1-3)

Description: Two permineralized leaves have been identified at the Eden Main localities that are triangular in transverse section. The adaxial corner has an angle of *ca* 72 degrees that suggests these leaves were borne in fascicles of five, but no fascicle sheaths are

known. Leaves are 0.9 mm in tangential and 1.0 mm in radial diameter. The leaves are of unknown length as only a few peels of each specimen were made.

The vascular strand is double, (Plate 13 Figs. 1-2). Bundles are separated by a band of sclerenchyma, *ca* two cells thick, that joins the sclerotic sheath that is one to three cells thick and surrounds the vascular bundles (Plate 13, Fig. 1). Phloem and cambium are not preserved and are represented by a gap abaxial to the xylem, between xylem and the transfusion tissue (Plate 13, Figs. 1-2). Secondary xylem is *ca* 5-7 cells thick and *ca* 8-10 rows wide. Tracheids are 18-24 μm in diameter. The transfusion tissue consists of one to three layers of round to ovoid cells, 24-45 μm in diameter in transverse section (Plate 13, Fig. 1). The endodermis is composed of a single layer of cells, circular in transverse section, 36-66 μm in diameter with thickened walls (Plate 13, Figs. 1-2). The mesophyll is not well preserved, but appears to be only *ca* one cell thick. The mesophyll cells are parenchymatous, and up to 48 μm in diameter with no plications observed (Plate 13, Figs. 1-2). The hypodermis is uniform (Harlow, 1931) and 3-8 cells thick (Plate 13, Fig. 1). The hypodermis contains sclerotic cells, 12-18 μm in diameter. Three external resin canals are visible in one specimen (Plate 13, Fig. 2) and are 60-90 μm in diameter. The epidermis is composed of thick-walled cells, circular in transverse section, 15-21 μm in diameter. Epidermal cells have a thick cuticle up to 6 μm thick (Plate 13, Fig. 3). Stomata have not been observed.

Occurrence: Eden Quarry: P14347 E bot; P14439 B bot.

Discussion: These fossil pine leaves share characters of the section *Trifoliae* (*sensu* Gernandt et al., 2005), or in other classifications *Pinus*, Section *Diploxylon* (Koehne, 1893; Shaw, 1914; Pilger, 1926) or section *Pinus* (Critchfield and Little, 1966). Leaves

of pines in the recently erected section *Trifoliae* have leaves with two vascular bundles, two to five (8) needles per fascicle and septal, internal, medial or rarely external resin canals (Gernandt et al., 2005). Leaves of pines that are placed into the more accepted sections Diploxylon or *Pinus* contain two or more resin canals (Harlow, 1931). The Eden Main fossil leaves share characters with these sections as they have leaves with two vascular strands, were apparently borne in fascicles of five and had external resin canals (Table 4). There are no extant pines with leaves borne in fascicles of five, two vascular bundles, and external resin canals. Excluding the position of resin canals, the Eden Main fossil leaves are similar to leaves of *Pinus paulustris, P. montezumae* and other members of the subsections *Australes* and *Ponderosae* (*sensu* Gernandt et al., 2005).

The fossil record of Pinaceae extends to the Early Cretaceous (e.g., Alvin, 1960; Stockey and Wiebe, 2008), some of the described fossils are reproductive structures, but there are several examples of anatomically preserved *Pinus* or *Pinus*-like leaves described from the fossil record (Jeffrey, 1908; Hollick and Jeffrey, 1909; Stopes and Kershaw, 1910; Ogura, 1932a; Penny, 1947, Miller, 1973, 1992; Robison, 1977a, 1977b; Ueda and Nishida, 1982; Stockey, 1983, 1984; Stockey and Nishida, 1986; Stockey and Ueda, 1986; Gandolfo et al., 2001, Stockey and Wiebe, 2006). There have been 12 permineralized Cretaceous pines described (Table 4) based on leaves. Of these, three five-needled pines have been described (Table 4); *Pinus quinquefolia* Hollick and Jeffrey from the Late Cretaceous of the eastern United States (Hollick and Jeffrey, 1909; Penny, 1947; Robison, 1977b), *P. pseudostrobifolia* Ogura emend. Stockey et Nishida (Ogura, 1932a, Stockey and Nishida, 1986) and *P. hokkaidoensis* Stockey et Ueda (1986), both from the Late Cretaceous of Japan.

Leaves of *Pinus quinquefolia* has an I-shaped fibrous band separating two vascular bundles. It has a thick-walled endodermis, plicate mesophyll, two to nine medial or external resin canals and a uniform hypodermis (Hollick and Jeffrey, 1909; Robison, 1977b). Among the characters present in the Eden Main leaf that separate it from *Pinus quinquefolia* are, a complete sclerotic bundle sheath, a lack of plicate mesophyll and only three resin canals (Table 4).

Pinus hokkaidoensis has leaves with an I-shaped band separating the two bundles, thin-walled endodermis, one to three layers of slightly plicate mesophyll, two external resin canals, one to four layers of uniform hypodermis, and thick-walled epidermis. The presence of I-shaped bundle sclerenchyma, plicate mesophyll, and three to eight layers of mesophyll in *Pinus hokkaidoensis*, separate it from the Eden Main five-needled pine leaves (Table 4).

The internal anatomy of the leaves of *Pinus pseudostrobifolia* is not well preserved, but there is a sheath present that may be similar to the sclerotic bundle sheath in the Eden Main fossil leaves (Ogura, 1932a; Stockey and Nishida, 1986). The leaves of *Pinus pseudostrobifolia* have two to three layers of uniform hypodermis (three to eight in the Eden leaves), and thick-walled epidermis, but appear to lack an endodermis, unlike the Eden Main leaves that have a discernable endodermis (Table 4).

A five-needled pine leaf, figured by Jeffrey (1908, Pl. XIV, Fig. 23) appears to be similar in shape to the Eden Main specimen. The leaf is not described in detail, but some observations can be made from the figure. The leaf appears to have two vascular bundles, and two or three external resin canals, munch like the Eden Main fossil leaves.

All of the fossil five-needled pines with good preservation show at least some plication in the mesophyll (Table 3). Plications have not been observed in the Eden Main leaves. The Eden Main fossil has a much thicker hypodermis than any previously described leaf (Table 3) and probably represents a new species.

Table 4. Comparison of anatomically preserved leaves of Cretaceous *Pinus* L.

Taxon	Needles/ fascicle	# Vascular bundles	V.B. Sclerenchyma	# Mesophyll Layers	Plicate	# Resin Canals	R.C. Placement	# Hypo.[1] Layers	Stomatal Location	Epidermal cells	Endodermis
P. yezoensis	1	1	Few cells	2-3	Y	2	External	2-3	Scattered	Roundish	Round, even thickness
P. flabellifolia	3	2	I-shaped	1-2	Slightly	2	External	1-4	Amphistomatic	Elliptical	Round, even thickness
P. pachydermata	3	2	Heart-shaped sheath	1-2	N	—	—	6	—	—	—
P. pseudoflabellifolia	3	2	?	2-3	Y	1(2)	External	2-3	—	—	Thin-walled
P. bifoliata	2-3	2	Absent	1-3	Slightly	2	External	1-3	Amphistomatic	Ellpitical	Thin-walled
P. triphylla	3	2	Band, narrow	5-6	Slightly	2-4	External	—	—	Oval, thick-walled	Thick-walled
P. haboroensis	3-4	2	I-shaped	2-5	Y	6-8	Medial/ External	1-4	Amphistomatic	Crescent shaped, thick-walled	Irregular outline, thick-walled
P. tetraphylla	4	2	Sheath	—	—	—	—	—	—	—	—
P. pseudotetraphylla	4	2	Sheath	1-2	Y	3	External	6	—	Square-polygonal	—
P. quinquefolia	5	2	I-shaped	3-4	Y	2-8	Medial/ External	—	—	Oval to angular	Thick-walled
P. hokkaidoensis	5	2	Thin, I-shaped	1-3	Slightly	2	External	1-4	Amphistomatic beaked	Oval to ellpitical	Thin-walled
P. pseudostrobifolia	5	2	Sheath	—	—	—	—	2-3	—	—	—
Eden 5-needled pine	5	2	Sheath	1	N	3	External	3-8	—	Square	Round, thick-walled
Eden 3-needled pine	3	2	I-shaped	1-2	Y	2	External	—	—	—	Round, thick-walled

Modifed from Stockey and Nishida (1986); data taken from Jeffrey (1908, 1910), Stopes and Kershaw (1910), Ogura (1932), Penny (1947), Robison (1977b), Udea and Nishida (1982), Stockey and Udea (1986), Stockey and Nishida, 1986). ?= unknown 1 Hypodermal

All species are from the Upper Cretaceous of Hokkaido, Japan except *P. quinquefolia* , *P. tetraphylla* , and the Eden Main specimens, all from the Upper Cretaceous of North America.

Three-needle pine leaves

(Plate 13, Figs. 4-5)

Description: Two leaves are known with an adaxial corner angle of *ca* 120 degrees that suggests the leaf came from a three-needled fascicle. However, the fascicle sheath is unknown. The leaf is 0.7 mm in radial and 1 mm in tangential diameter. The vascular strand is double, separated by a narrow band of sclerenchyma that becomes T-shaped with the wide end on the abaxial side (Plate 13, Fig. 4). The sclerenchyma as well as the surrounding tracheids are not well preserved. The phloem and cambium are not preserved and are represented by a gap in the tissues. The transfusion tissue is one to three cells thick and consists of cells round to oval in transverse section, 30-40 µm in diameter (Plate 13, Fig. 4). Pitting has not been observed in cells of the transfusion tissue. The endodermis consists of a ring of cells, circular in transverse section, and 30-50 µm in diameter (Plate 13, Fig. 4). The mesophyll contains plicate parenchymatous cells *ca* 30 µm in diameter with dark contents (Plate 13, Figs. 4, 5). The mesophyll is 1-2 cells thick, thicker at the corners. Two external resin canals are visible near the abaxial corners, 30-50 µm in diameter (Plate 13, Figs. 4, 5). Hypodermis and epidermis are represented by an amorphous layer, about 15-24 µm thick.

Occurrence: Eden Quarry: P14460 E top, G top.

Discussion: Plants with three leaves per fascicle, leaves with two vascular bundles and external resin canals, are found in the Pinaceae, Section *Pinus* (e.g., Gernandt et al. 2005). The two vascular bundles are like those in section *Diploxylon* (Koehne, 1893; Shaw, 1914; Pilger, 1926) or section *Pinus* (Critchfield and Little, 1966) in different classification systems.

There are a few similar fossil three-needled pines known from the Cretaceous (Jeffrey, 1908; Hollick and Jeffrey, 1909; Ogura, 1932a; Ueda and Nishida, 1982). As well as a few pines that usually have five needles and occasionally have three (Ueda and Nishida, 1982; Stockey and Nishida, 1986).

Jeffrey (1908) illustrated an unnamed three-needled pine from the Cretaceous of eastern North America. It has two vascular bundles, at least three layers of mesophyll and two medial or external resin canals (Jeffrey, 1908). This leaf can be separated from the Eden Main three-needled pine because the Eden leaves have only one to two mesophyll layers.

Leaves of *Pinus flabellifolia* Ogura (1932a) emend. Stockey et Nishida (1986) is known from the Late Cretaceous of Japan. In transverse section *Pinus flabelifolia* leaves have an I-shaped sclerotic strand between the vascular bundles, circular, thick-walled endodermal cells, one layer of indistinctly plicate mesophyll, and two resin canals located near the lateral corners and partially embedded in the thick-walled hypodermis (Ogura, 1932a). The mesophyll in *Pinus flabellifolia* is only slightly plicate, while that of the Eden Main leaves are strongly plicate (Table 3).

Pinus pachydermata Ueda et Nishida (1982) has leaves with a heart-shaped sclerotic bundle sheath, thin-walled endodermis, one to two layers of non-plicate mesophyll, and an irregular hypodermis, six cells thick. The Eden Main three-needled pine leaves lack a bundle sheath and have only an I-shaped sclerenchyma strand (Table 4). Also, the Eden Main leaves have plicate mesophyll while *Pinus pachydermata* does not (Table 4).

Pinus pseudoflabellifolia Ueda et Nishida (1982) has thin-walled endodermis, two to three mesophyll layers with plicate cells, *ca* one external resin canal, two to three layers

of uniform hypodermis. The Eden Main leaves have one to two layers of mesophyll, while *Pinus pseudoflabellifolia* leaves have two to three layers of mesophyll (Table 4).

Leaves of *Pinus triphylla* Hollick and Jeffrey (1909) (Robison, 1977b) have a narrow band of sclerenchyma separating the vascular bundles, five to six layers of slightly plicate mesophyll (1-2 in the Eden Main leaves), thick-walled endodermis, two to four external resin canals, and a uniform hypodermis (Table 4).

Pinus bifoliata Ueda et Nishida (1982) emend. Stockey et Nishida (1986) has leaves borne in fascicles of two or three, have no sclerenchyma associated with vascular bundles, thin-walled endodermis, one to three layers of slightly plicate mesophyll, two external resin canals and one to three layers of uniform hypodermis (Table 4). The lack of bundle sclerenchyma, separate these leaves from the Eden main specimen (Table 4).

Pinus haboroensis Stockey and Nishida (1986) has leaves borne in fascicles of three and four, an I-shaped sclerenchyma strand, two to five layers of plicate mesophyll (one to two in the Eden Main leaves), six to eight median or external resin canals (two in the Eden Main leaves), and one to four layers of uniform hypodermis (Table 4).

The Eden Main fossil leaf can be separated from most described fossil taxa on the basis of one or more characters. The Eden Main leaves seem to be most similar to those of *P. flabellifolia* (Table 4).

Pinaceous pollen cone

(Plate 14, Figs. 1-4; Plate 15, Figs. 1-4)

Description: A single isolated pollen cone containing bissaccate pollen is known from the Eden Main localities. The cone appears to be bent in the matrix, revealing part of the apical end in longitudinal and part of the basal end in transverse section (Plate 14, Fig. 1)

and is up to 1.8 mm wide and at least 6.2 mm long. Microsporophylls contain one vascular bundle (Plate 14, Fig. 2). Each sporophyll bears two abaxial pollen sacs (Plate 14, Fig. 2). The outer layer of some pollen sacs have conspicuous helical wall thickenings. Most of the pollen sacs contain bisaccate grains (Plate 14, Fig. 4; Plate 15, Figs. 1-2). In equatorial view pollen grains up are up to 80 μm in diameter. The corpus is 45-60 μm in diameter, and the sacci are 20 μm wide and up to 40 μm tall. The corpus appears to have a spinulose sculpture (Plate 15, Fig. 3). Sulcus sculpturing is unknown. The sacci are abraded, often leaving the internal endoreticulations visible (Plate 15, Fig. 4). These extend up to 4.0 μm into the saccus and are about 2-4 μm apart.

Occurrence: Eden Main 2nd Ditch: P14468 F bot and G top.

Discussion: The presence of two pollen sacs per sporophyll and bisaccate pollen suggest an affinity with the Pinaceae (Sporne, 1965) for this pollen cone. Pollen cones are rare in the fossil record. This is likely because they quickly decay and are not sturdy enough to remain intact during long transport prior to fossilization (Miller, 1992). The Eden Main fossil cone appears to be fairly intact which indicates it did not travel far before being deposited and preserved. A few pollen sacs appear to be empty. This, along with the presence of mature pollen and endothecial thickenings on the outer layer of the pollen sac walls (Gifford and Foster, 1989; Phipps et al., 1995), indicates that the cone was probably mature at the time of preservation.

Anatomically preserved conifer pollen cones with affinities to extant families are rare in the fossil record. The few pinaceous specimens that are known come from the Miocene of Washington state (Miller, 1992), the Eocene of British Columbia (Phipps et al., 1995), the Late Cretaceous (Turonian) of New Jersey (Gandolfo et al., 2001) and the

Late Cretaceous of India (Kapgate et al., 2007). Another possible pinaceous pollen cone is known from the Coniacian of Japan (Takahashi et al., 1999b), but pollen has not been found. Classifying the Eden Main cone is difficult because characters that would allow the pollen to be placed into a genus, e.g., minute cappa (proximal side of the corpus), cappula (distal side of the corpus) and sacci characters (Baghell, 1975) have not been observed. However, the "honeycomb" endoreticulation of the bladders and size of the sacci relative to the corpus appears to be most similar to the genus *Pinus* or *Picea* (Ueno, 1958). It should be noted that Podocarpaceae can also have pollen cones with two pollen sacs per sporophyll and bisaccate pollen that can be easily confused with pine pollen (Reinink-Smith and Leopold, 2005). However, no other potential podocarpaceous fossils are known from the Eden Main localities. Further preparation and study will be required to properly classify this cone.

Family: Cupressaceae

Twigs with attached leaves

(Plate 16, Figs. 1-3)

Description: The most abundant of all identifiable fossils at the Eden Main fossil localities are vegetative remains of Cupressaceae, consisting of isolated leaves and twigs with attached leaves (Plate 16, Figs. 1-3). Leaves are helically arranged on twigs (Plate 16, Fig. 1), are needle like (Plate 16, Fig. 2) and rhomboidal in transverse section. Secondary xylem of twigs seen in transverse section lack resin canals and is similar to abundant wood fragments that are found throughout concretions from all of the Eden Main localities (Plate 16, Figs. 2-3).

Leaves are 0.7-2.0 mm wide, 0.4 mm-1.0 mm thick, and when measurable, are at least 1.0 cm long. At the center of each leaf is a single large resin canal (Plate 16, Fig. 1). Smaller marginal canals, have not been observed. Mesophyll can be loosely to densely packed. Vascular/transfusion tissue and epidermis are not well preserved in any of the specimens that have been closely observed.

Occurrence: Ubiquitous at the Eden Main localities. Figured specimens: Eden Quarry; The Ditch: P14334 D; P14492 D.

Discussion: Helically arranged rhomboidal leaves with a single central resin canal, attached to twigs with secondary xylem that lacks resin canals suggest affinities to taxodiaceous Cupressaceae (e.g., Farjon, 2005b). These vegetative remains are found in almost every concretion from the Eden Main localities.

The Cupressaceae are very common in Cretaceous strata (e.g., Crane, 1987; Stockey et al., 2005). It is possible that there is more than one taxodiaceous leaf type present at the Eden Main localities because some observed leaves have slightly different shapes in transverse section. This could also be due to different levels of section. Only when several leaves are throughly peeled will leaf diversity at the localities be completely understood.

Taxodiaceous twigs with attached pollen cones

(Plate 16, Figs. 4-6)

Description: One specimen of a branching twig with attached leaves and pollen cones is known. Cones are 1.9 mm wide and consist of a central axis with attached sporophylls, cones are surrounded by skeletonized ensheathing leaves (Plate 16, Fig. 4).

The skeletonized ensheathing leaves are rhomboidal in transverse section, 1.6-2.0 mm wide and 0.5-0.9 mm tall and contain a single central resin canal, 0.2-0.4 mm in diameter. Ensheathing leaves have poorly preserved internal tissues (Plate 16, Fig. 4).

Microsporophylls are helically arranged, and the shape of the sporophyll is unknown (Plate 16, Fig. 4). Each microsporophyll bears at least four ellipsoidal, abaxial pollen sacs (Plate 16, Fig. 5). Pollen sacs have endothecial thickenings on their outer walls (Plate 16, Fig. 6).

Pollen grains are 24-30 μm in equatorial diameter, and are common in most of the pollen sacs. Pollen grains are subspheroidal, nonsaccate, and appear to lack papillae (Plate 16, Fig. 8).

Occurrence: Eden Quarry: P14440 C top; P15037 B bot, and C top.

Discussion: The leaves attached to twigs with cones are similar to those described above, indicating an affinity with taxodiacious Cupressaceae. There are only four permineralized taxodiaceous pollen cones described from the fossil record, three from the Tertiary (Rothwell and Basinger, 1979; Matsumoto et al., 1997; Hernandez-Castillo et al., 2005) and one from the Cretaceous (Serbet and Stockey, 1991). One other cone of probable cupressaceous affinity is known from fusainized remains from the Coniacian of Japan (Takahashi et al., 1999b) but it has not been described in detail.

Taxodiaceous leaf, *cf. Cunninghamia* R. Br.

(Plate 16, Figs. 7-8)

Description: A single specimen of a conifer leaf in cross section that is triangular in shape (Plate 16, Fig. 7) is known. The leaf is 1.8 mm wide by 0.5 mm thick. A single large central resin canal is present and abaxial to winged-shaped transfusion tissue (Plate

16, Fig. 8). The transfusion tissue is composed of parenchyma, 15-45 μm in diameter. Pitting has not been observed on cell walls. Tracheids are 6 μm in diameter (Plate 16, Fig. 8). Mesophyll is parenchymatous with cells, 30-60 μm in diameter, some cells appear to have dark contents that may be fungal hyphae. No obvious hypodermis has been observed. The epidermis is composed of cells that are square in cross section, up to 18 μm in diameter. Stomata are not preserved, but cavities on the adaxial surface suggest that further peeling may reveal their arrangement.

Occurrence: Eden Quarry: P14320 B bot.

Discussion: Permineralized *Cunninghamia*-like fossils are known from the Cretaceous (Serbet, 1997; Stockey et al., 2005, Brink et al., 2007) and the Oligocene (Miller, 1990) of North America. Two extant species, *Cunninghamia lanceolata* Lambert and *C. konishii* Hayata are found in Asia (Farjon, 2005a). The anatomy of *C. konishii* has not been well studied, but *C. lanceolata* has wing-shaped transfusion tissue similar to the Eden Main fossil and one large and up to two smaller resin canals (Cross, 1941; Miller, 1990; Serbet, 1997). The Eden Main fossil differs from *Cunninghamia lanceolata* and leaves of *Cunninghamiostrobus* Miller et Crabtree, an Oligocene, North American fossil (Miller, 1990), as it appears to lack a thick hypodermis (Cross, 1941). More leaves and/or reproductive structures will greatly aid in the taxonomic placement of this leaf.

Conifer seed, *cf. Araucaria*

(Plate 17, Figs. 1-3)

Description: Two conifer seeds with basally attached nucellus and thick sclerotesta (Plate 17, Figs.1-2) have been found at the Eden Main localities. Seeds are 4-7 mm in diameter and 7-10 mm long. The outer edge of the sclerotesta is abraded, and sarcotesta

is not preserved. The sclerotesta is up to 2 mm thick, composed of thick-walled sclereids up to 30 μm in diameter that form zig-zag patterns (Plate 17, Fig. 2). The endotesta is composed of poorly preserved parenchymatous cells and is 0.2-0.4 mm thick (Plate 17, Fig. 3). The nucellus is cellular and appears to be attached to the chalazal end of the integument, with the micropylar end free and has a wavy apex (Plate 17, Figs. 1, 3). Inside the nucellus is the possible remains of the megagametophyte (Plate 17, Fig. 3).

Occurrence: Eden Main 2nd-Ditch; Eden Quarry: P14465 D top, C bot; P14467 E.

Discussion: Seeds with an free wavy nucellar apex are known in extant (Eames, 1913) and extinct araucarian conifers (Darrow, 1936; Stockey, 1975, 1978, 1994; Stockey et al., 1994; Cantrill and Raine, 2006). Extant araucarian conifers are mostly restricted to the Southern Hemisphere, but fossil members are known from northern localities (e.g., Stockey, 1994). The dinoflagellate cysts or acritarchs described in Chapter 2 have been found inside of one seed and probably washed into the micropyle after the seed fell or was washed into the ocean.

Subdivision: Angiospermophytina

Order: Laurales

Family: Lauraceae

Isolated Flowers

(Plate 18, Fig. 1)

Description: Isolated pedicellate, bisexual flowers have been identified (Plate 18, Fig. 1). Flowers are up to 4.0 mm tall and 2.0 mm wide. The hypanthium is shallow and bears at least two whorls of tepals (Plate 18, Fig. 1). There are at least two (probably three) whorls of stamens (Plate 18, Fig. 1). Pollen is not preserved. Stamens of the inner whorl

are extrorse, while the outer whorls are introrse (Plate 18, Fig. 1). Anthers are borne on the end of an elongate filament at least 0.7 mm long (Plate 18, Fig. 1). There are two sporangia per anther. The gynoecium is superior, 0.8 mm tall and 0.4 mm wide, and monocarpellate (Plate 18, Fig. 1). The style is unknown. All floral organs bear idioblasts, up to 12 μm in diameter, sometimes containing dark contents.

Occurrence: The Ditch; Eden Quarry: P13527 B top; P14347 D bot; P14464 E bot 2.

Discussion: Trimerous flowers with two whorls of tepals, shallow hypanthia, superior ovaries, several whorls of stamens, and idioblasts throughout, suggest affinity with Lauraceae (Kostermans, 1957; Rohwer, 1993; Judd et al., 2002). There are with up to 3500 extant species (Rohwer, 1993) in this family, mostly found in the tropics. Over 500 fossils with lauraceous affinities have been described (mostly leaf fossils) from the Early Cretaceous to the Late Tertiary (Eklund, 2000). Fossil lauraceous pollen is virtually unknown, but this is not surprising because the exine of extant lauraceae is weakly developed making preservation unlikely (MacPhail, 1980; Muller, 1981; Herendeen et al., 1994). Characters that are often used to distinguish fossil members of the family include: number of stamens, number of staminal whorls, number of sporangia per anther, direction of anther dehiscence, the presence or absence of an innermost staminodal whorl and receptacle shape (e.g., Kostermans, 1957; Judd et al., 2002; Little, 2006). The Eden Main fossil flowers are known only from a few sections, making complete comparisons currently impossible. The presence of a shallow hypanthium, bisexuality, *ca* three whorls of stamens, the outer whorls with introrse and the inner with extrorse dehiscence, do not provide enough detail to compare or contrast the Eden Main flowers with many described extant or fossil lauraceous taxa. The conservation of floral characters in

Lauraceae provide difficulty even for the identification of extant taxa (e.g., Kostermans, 1957).

Isolated Inflorescences

(Plate 18, Figs. 2-4)

Description: Three inflorescences are known from the Eden Main localities. Inflorescence axes are broken and the original length is unknown, but they are at least 3.9 mm long. The most completely preserved specimen displays ten flowers in longitudinal section (Plate 18, Fig. 2); floral arrangement on the inflorescence axis is impossible to ascertain with the sections available.

Flowers are attached to a central axis. With current sections it is difficult to tell if the flowers are pedicellate or sessile (Plate 18, Figs. 2, 4). One inflorescence is known in transverse section, but bears flowers that are too immature to interpret the arrangement of floral parts (Plate 18, Fig. 4). Most of the flowers of inflorescences are sectioned in oblique longitudinal section and are not well preserved. Two apical flowers on one inflorescence appear to be cut in oblique transverse section (Plate 18, Figs 2, 3). In all inflorescences each flower is subtended by an overarching bract (Plate 18, Figs. 2, 4). Flowers are up to 1.0 mm long and 0.9 mm wide, and have at least two perianth whorls (Plate 18, Fig. 3). The inner whorl of stamens are not well preserved, but the outer whorls appear to be introrse (Plate 18, Fig. 3). There were probably two sporangia per anther (Plate 18, Fig. 3). At the center of each flower is a gynoecium.

The inflorescence axis, bracts and flowers contain numerous large cells , up to 36 μm in diameter, interpreted as idioblasts. These cells often contain brown contents (Plate 18, Figs. 2-4). The inflorescence axis, bracts, and flowers are covered with numerous

uniseriate, unbranched trichomes (Plate 18, Figs. 2, 4). Trichomes are more dense on the inflorescence axis and bracts than on the floral parts.

Occurrence: Eden Quarry; Eden Main Ditch: P13527 I; P14400 C bot; P14464 B bot.

Discussion: The presence of flowers with introrse and extrorse stamens, and organs with trichomes and idioblasts are characteristic of Lauraceae (e.g., Rohwer, 1993). Though the flowers found in infloresences are not well preserved, they appear to have an arrangement of parts similar to the isolated lauraceous flowers known from the Eden Main localities. Most inflorescence types in the Lauraceae are racemose (Rohwer, 1993). It is difficult to ascertain the presence of pedicels on the flowers either due to section view or floral maturity. Despite the quality of preservation, the Eden Main inflorescences can be separated from *Mauldinia* Drinnan, Crane Friis et Pederson, a widespread Late Cretaceous lauraceous taxon that has a unique flattened bilobed inflorescence with sessile flowers (Drinnan et al., 1990; Eklund and Kavček, 1998; Herendeen et al, 1999; Frumin et al., 2004). Further inflorescence and floral characters will be required before these infloresences can be thoroughly compared to those of extant and fossil lauraceous taxa.

Lauraceous fruit

(Plate 19, Figs. 1-4)

Description: One isolated fruit, roughly urceolate in longitudinal section, with overarching fleshy perianth parts (Plate 19, Fig. 1), and a receptacle that is swollen into a shallow cupule (Plate 19, Fig. 1) has been identified from the Eden Main localities. The fruit is 4.0 mm long and 3.5 mm in diameter, with a single apically attached ovule (Plate 19, Fig. 1, 3). The integument is 84 μm thick with square to rectangular cells up to 18

μm in diameter (Plate 19, Fig. 1, 3, 4). The apex of the ovary contains fungal hyphae that appear to have degraded the integument (Plate 19, Fig. 3). A discontinuous palisade endocarp 0.14 mm thick is located outside of the integument (Plate 19, Fig. 3). Outside of the endocarp is a fleshy mesocarp (Plate 19, Fig. 1, 3, 4). The mesocarp is 0.60 mm thick, composed of parenchymatous cells up to 120 μm in diameter, and idioblasts with dark contents *ca* 120 μm in diameter (Plate 19, Fig. 1, 3, 4). Between the mesocarp and the tepals are degraded remnants of stamens (Plate 19, Fig. 4). The outer two layers of tepals are fleshy, and overarch the fruit (Plate 19, Fig. 1). Tepals contain vascular strands with scalariform secondary wall thickenings (Plate 19, Fig. 2). Parenchyma and idioblasts of the cupule and tepals are similar to those of the outer mesocarp.

Occurrence: Eden Quarry: P14465 B bot.

Discussion: Fruits with a single apically attached ovule, palisade endocarp, a swollen receptacle forming a cupule and numerous idioblasts are diagnostic of the Lauraceae (e.g., Kostermans, 1957; Eklund, 2000). The fossil fruit appears to be near maturity as the palisade layer is well defined and the seed integument is thick, but without a developmental series it is impossible to know how long the tepals persisted on the fruit. Some lauraceous fruits are almost entirely enclosed by a persistent cupule (Rohwer, 1993), but the Eden Main fruit has only a shallow cupule. The structures enclosing the fossil fruit appear to be perianth parts. A few extant genera such as *Dicypellium* Nees et Mart., *Licaria*, Aubl., *Neocinnamomum* Liou Ho, and *Paraia* Rohwer, Richter et van der Werff often have tepals that are still attached on the mature fruit, and are enlarged at maturity (Rohwer, 1993). The anatomy as well as the developmental sequence of the

Eden Main fruit need to be more completely understood before it can be compared to extant Lauraceae.

A early Coniacian fossil fruit from Japan figured as "hypogenous flower type two" by Takahashi et al,, (1999b) has persistent perianth parts that may have covered most of the fruit at maturity. These flowers/fruits are *ca* 1.2 mm long and 1.2 mm wide and have two whorls of three tepals each, borne on a shallow cupule (Takahashi et al., 1999b). When anthers are found they are tetrasporangiate, but when anthers are present, the gynoecium is not discernable, suggesting the flowers were unisexual (Takahashi et al, 1999). The Eden Main fruit is larger than the Japanese specimens and appears to have developed from a bisexual flower.

A lauraceous fruit comparable to the Eden Main fruit is *Crowella globosa* Reid et Chandler from the Eocene London Clay flora. *Crowella* is almost entirely enclosed by perianth parts that are fused internally to each other, but free from the fruit wall (Reid and Chandler, 1933). This fruit has an enlarged, shallow receptacle like the Eden Main fruit, and a similar shape in longitudinal section. Reid and Chandler (1933) noted that there were no known living members of the family that had perianth parts that were as large as those seen in *Crowella*, nor were there any extant taxa with perianth parts that were fused internally and free externally. The tepals of the Eden Main fruit appear to not be fused in the sections that have been examined so far.

Discontinuous endocarp like that seen in the Eden Main fossil has also been noted in two fossil taxa that are assignable to extant genera, *Endiandra* Brown and *Beilschmiedia* Nees from the Eocene London Clay. However, like the Eden Main fruit, this may be due to incomplete preservation and is not a useful taxonomic character (Reid and Chandler,

1933). Similar breaks in the endocarp in "*Similkamena borealis*" Little et Stockey from the Eocene of British Columbia are thought to have been caused by degradation (Little, 2006).

Lauraceae

Angiosperm wood *cf. Paraphyllanthoxylon*

(Plate 20, Figs. 1-5; Plate 21, Figs. 1-4; Plate 22, Figs. 1-4)

Description: Angiosperm wood remains known from an abraded permineralized axis as well as at least 50 smaller permineralized and fusainized fragments. The largest axis is 4.1 cm in diameter and at least 10 cm long. Growth rings are absent. The pith is mostly crushed and appears to have been composed of thin-walled parenchyma intermixed with sclerenchyma (Plate 20, Fig. 2). Axial parenchyma is paratracheal (Plate 20, Fig. 5). The vessels are solitary or in radial groups of two to five with diffuse porous arrangement (Plate 20, Figs. 3-5; Plate 21, Fig. 2). Vessel to ray pitting consists of circular to oval pits, 12-15 μm in diameter (Plate 21, Fig. 4). Wood fibers are septate (Plate 22, Fig. 4). Ray cells are procumbent, homocellular, 18-66 μm in radial diameter and 24-30 μm in tangential diameter (Plate 21, Fig. 1, 2; Plate 22, Figs. 1, 2, 4). Rays are 8-25 cells tall (0.92- 3.2 mm) and 2-5 cells wide (0.09-0.6 mm) (Plate 22, Figs. 1, 2, 4). There are roughly 18 vessels per mm^2 that are 36-180 μm in tangential diameter, and 204-276 μm long (Plate 22, Fig. 1). Intravascular pitting in tracheary elements is alternate and consists of circular, simple pits 9-12 μm in diameter (Plate 22, Fig. 3). Vessels have simple, oblique perforation plates (Plate 22, Fig. 2), and abundant tyloses (Plate 20, Figs. 3-5; Plate 21, Figs. 2-3).

Occurrence: Known from all localities. Figured specimens: Eden Quarry: P14457 E top; P15041 A.

Discussion: Late Cretaceous diffuse-porous wood, with abundant tyloses, septate fibers and lacking growth rings is assignable to the genus *Paraphyllanthoxylon* Bailey (e.g., Herendeen, 1991). Several species are known from the Early Cretaceous to the Paleogene (e.g., Bailey, 1924; Ogura, 1932b; Spackman, 1948; Mädel, 1962; Cahoon, 1972; Thayn et al., 1983; Herendeen, 1991; Wheeler, 1991; Meijer, 2000).

There are seven species of Cretaceous *Paraphyllanthoxylon* known from permineralized and fusainized specimens. These include: *Paraphyllanthoxylon utahense* Thayn, Tidwell et Stokes; *P. idahoense* Spackman; *P. marylandense* Herendeen; *P. arizonense* Bailey; *P. alabamense* Cahoon; *P. illinoisense* Wheeler all from North America, and *P. capense* Mädel from South Africa (see Herendeen, 1991 for review). Eden Main fossil dicot wood may be separated from some of the known Cretaceous specimens based on a few of the known wood characters. The vessel element length in the Eden Main wood (204-276 μm) is much shorter than in *Paraphyllanthoxylon alabamense* (500-700 μm), or *P. illinoisense* (610-1200 μm) (Herendeen, 1991). The lack of vertical fusion of rays separates the Eden fossil from *Paraphyllanthoxylon marylandense*, and the lack of uniseriate rays separates the Eden fossil from *P. arizonense* (Herendeen, 1991). Vessel density in the Eden Main fossil (18 vessels per mm^2) is less than *Paraphyllanthoxylon capense* (24-60/mm^2), and slightly more then *Paraphyllanthoxylon utahense* (12/mm^2) (Herendeen, 1991). A more thorough study of the Eden Main fossils will be required to determine the relationship of the Eden Main fossil to *Paraphyllanthoxylon idahoense*. The width of the rays is slightly different than

in the Eden Main specimen, two to five cells wide in the Eden Main specimen and two to four in *P. idahoense* (Herendeen, 1991).

The affinities of *Paraphyllanthoxylon* are unknown but Lauraceae and Euphorbiaceae as well as other families have been suggested as possibilities (see Herendeen, 1991). Herendeen (1991) states that *Paraphyllanthoxylon marylandense* wood can be matched to wood of the inflorescences of *Mauldinia mirabilis* Drinnan, Crane, Friis et Pederson, a lauraceous inflorescence. The wood of *Paraphyllanthoxylon* species differ from most lauraceous wood as lauraceous wood generally has abundant axillary parenchyma and secretory cells (Herrendeen, 1991). Therefore, except for *P. marylandense*, the affinities of species of *Paraphyllanthoxylon* remain in doubt (Herendeen, 1991).

Order: Proteales

Family: Platanaceae

Isolated Infloresences

(Plate 23, Figs. 1-5; Plate 24 Figs. 1-4)

Description: Four platanaceous inflorescences are known from the Eden Main localities (Mindell et al., 2006a). Pedunculate globose inflorescences are up to 4.1 mm in diameter and bear *ca* 30 flowers. Inflorescences probably bear both perfect and imperfect flowers on a parenchymatous receptacle (Plate 23, Fig. 1). Flowers are up to 1.0 mm long and 0.5 mm in diameter. It is difficult to tell whether all or only some of the flowers in the inflorescences are functionally bisexual. The unisexual flowers are essentially identical to the bisexual flowers except that only the gynoecium or androecium is lacking. Whether these flowers were actually bisexual or if this is a result of preservation is unknown, therefore, the bisexual flowers will be described here. At maturity, each

flower has at least two whorls of tepals that overarch the flower (Plate 23, Fig. 3-4) (Mindell et al., 2006a). There are five bithecate stamens per flower that are up to 0.4 mm long and 0.3 mm wide that bear sclerotic apical extensions (Plate 23, Fig. 1), up to 0.4 mm long and 0.2 mm wide (Mindell et al., 2006a). Clusters of pollen are found in many pollen sacs (Plate 23, Fig. 5). Pollen is prolate (Plate 24, Figs. 1-3), tricolpate (Plate 24, Fig. 2) with a granular aperture (Plate 24, Fig. 2), and are up to 13 um in polar and 9 um in equatorial diameter (Mindell et al., 2006a). Pollen is tectate with microreticulate sculpturing (Plate 24, Figs. 1-4). Stamens with pollen are found on flowers that have carpels with enclosed ovules (Plate 23, Fig. 3). Each flower has five carpels, up to 0.7 mm long and 0.2 mm in diameter. They are glabrous, conduplicate (Mindell et al., 2006a) and triangular in transverse section with a median suture (Plate 23, Figs. 1, 3). Styles are undifferentiated, and mature carpels bear a single seed, each with a single wing (Plate 23, Fig. 4).

Occurrence: Eden Quarry: P14320 E bot; P14420 E bot; P14460 E bot, P14468 C bot, and D top.

Discussion: Flowers with a pentamerous arrangement on a pedunculate head with bithecate stamens with apical extensions, tricolpate, reticulate pollen, unilocular carpels, and undifferentiated styles allow for the placement of these Eden Main inflorescences in the Platanaceae (e.g., Manchester 1986, Crane 1989, Kubitzki, 1993).

Extant Platanaceae consists of 8-10 species in the genus *Platanus* L. (Nixon and Poole, 2003). Extant species in the family may have pedunculate inflorescences and apical staminal extensions (Nixon and Poole, 2003) like those in the Eden Main inflorescence. Flowers in some species of extant *Platanus* rarely have rudimentarily or

functionally bisexual flowers or inflorescences (Boothroyd, 1930; Schwarzwalder and Dilcher, 1981; Floyd et al., 1999). The Eden Main platanaceous fossils have a fixed pentamerous arrangement while the organization of extant *Platanus* is variable (e.g., Kubitzki, 1993). The Eden Main fossils have bisexual inflorescences and flowers. The winged seeds of the Eden Main fossil are not seen in extant *Platanus*. In extant *Platanus* a one-seeded achene subtended by long trichomes, is the dispersal unit (e.g., Judd, 2002). The seed is most likely the dispersal unit in the Eden Main fossil as the wing is prominent, the fruits are glabrous, and the carpels have a prominent longitudinal suture that was probably the location of dehiscence.

The family Platanaceae has recently been placed as the sister to Proteaceae, in a clade that is sister to Nelumbonaceae, based on molecular evidence (Hoot et al., 1999; Doyle and Endress 2000; Stevens, 2001 onwards; Hilu et al., 2003), with only a few supporting morphological characters (Doyle and Endress 2000; Hoot et al., 1999, Carpenter et al., 2005). Functionally bisexual flowers with winged seeds are typically lacking in extant and fossil Platanaceae, but present in extant Proteaceae (Cronquist, 1981; Judd et al., 2002). Nelumbonaceae, the family sister to the clade composed of Platanaceae and Proteaceae (Hoot et al. 1999; Doyle and Endress 2000; Stevens, 2001 onwards; Hilu et al. 2003), has bisexual flowers (Williamson and Schneider, 1993) and seeds with a prominent raphe (Watson and Dallwitz, 1992 onwards).

The oldest platanaceous flowers known in the fossil record are from the Early Cretaceous (Friis et al., 1988). It is common for Cretaceous and Paleogene platanaceous fossils to have five-parted flowers like those of Eden Main, but all known specimens are either unisexual, or only rudimentarily bisexual (both gynoecium and androecium

present, but only one is functional) (Manchester, 1986; Friis et al., 1988, Pigg and Stockey, 1991; Mindell et al., 2006b). The genus *Quadriplatanaus* is known from the Coniacian to Santonian of Georgia U.S.A., that is of similar age to the Eden Main fossils (Magallón-Puebla et al., 1997). Interestingly this fossil has seeds with a wing or raphe similar to the Eden main seeds, but *Quadroplatanus* has four-parted flowers, and is only rudimentarily bisexual (Magallón-Puebla et al., 1997). The Eden Main platanaceous fossils have a unique suite of characters and appear to represent a new genus of the Platanaceae.

Order: ?Saxifragales

Infructescence

(Plate 23, Fig. 6)

Description: A single specimen is known of an abraded infructescence with at least six fruits, each with two locules, visible in longitudinal section, attached to a common fleshy receptacle Plate 23, Fig. 6). The entire infructescence is 6 mm in diameter. Fruits are up to 0.4 mm in diameter. The receptacle is parenchymatous. Fruits are attached by a short peduncle (Plate 23, Fig. 6). The outer fruit wall is degraded and represented by black amorphous material. The inner fruit wall appears to be sclerotic and is up to 110 µm thick (Plate 23, Fig. 6).

Occurrence: Eden Quarry: P14470 D bot and E top.

Discussion: Fruits with at two locules arranged on a parenchymatous receptacle are found in the Saxifragales, e.g., Altingiaceae (Judd et al., 2002), an order that extends to at least the Turonian (Zhou et al., 2001). Fruits in several families in the Saxifragales have two-carpellate capsules that, like those in the Eden Main fossil, may be woody; however,

the carpels in this order tend to be only partially connate (Judd et al., 2002) as opposed to fully fused as in Eden Main fossil. Further preparation to determine if the fruit is definitely two-loculed, and other morphological features will greatly improve the ability to classify this infructescence.

Order: Cornales

Family Nyssaceae (Cornaceae (*sensu* Eyde, 1988))

Three-four loculed fruits

(Plate 25, Figs. 1-3)

Description: At least 10, three to four loculed fruits with valvate dehiscence are known from the Eden Main fossil localities (Plate 25, Figs. 1, 2, 4). Fruits are up to 3 mm in diameter. The endocarp is often ridged (Plate 25, Figs. 1, 4), up to 0.54 mm thick, and composed of elongate sclereids up to 70 µm in diameter and *ca* 120 µm long (Plate 25, Fig. 5). The arrangement of vascular bundles is unknown in all specimens. Germination valves are seen in most fruits suggesting they may have been elongate as all fruits would have to be randomly sectioned towards the apex for short germination valves to be seen. In some fruits, locules are lined with square to rectangular cells 18 µm in diameter (Plate 25, Fig.5). Poorly preserved contents suggest each locule contained one seed.

Occurrence: Eden Quarry; Eden Ditch; Eden Main 2nd ; Eden Main 400 Ditch: P14472 C bot; P13037 C bot, E, P14600 B; P14574 A; P14468 B bot.

Discussion: These drupaceous three-to four-loculed fruits with germination valves are probably assignable to the Cornales (e.g., Judd et al., 2002; Takahashi et al., 2002). This order contains many families, most with drupaceous fruits, but recent phylogenetic analyses place three families (Hydrangaceae, Losaceae and Hydrostachyaceae) into the

Cornales that are distinguished from the Eden Main fruits by their thin-walled capsules (Xiang et al., 1993, 1998, 2002; Magallón et al., 1999, Xiang, 1999; Takahashi et al., 2002).

There are families (Cornaceae, Curtisiaceae, Nyssaceae) in the order that have sclerotic endocarps that are comparable to the Eden Main fruits (Takahashi et al., 2002). The genus *Cornus* L. (Cornaceae) may be distinguished from the Eden Main fossils as it tends to have one to two (rarely four) locules, and the endocarp is composed of isodiameteric sclereids (Takahashi et al., 2002) unlike the elongate sclereids/fibers in the Eden Main specimens. *Alangium* L. (Cornaceae) has one to two locules, and like *Cornus*, the endocarp is also composed of isodiametric sclereids, as is the endocarp in the four loculed fruits of *Curtisia* Aiton (Curtisiaceae) (Takahashi et al., 2002). *Davidia* Baill. (Nyssaceae) has a fibrous endocarp and elongate germination valves but has six to nine carpels (Manchester et al., 1999; Takahashi et al., 2002). *Camptotheca* Decne. (Nyssaceae) has a thin endocarp, and one to two locules (Manchester et al., 1999; Takahashi et al., 2002) . Three styles are present in *Camptotheca* that suggest three carpels are present (Manchester et al., 1999). *Nyssa* L. (Nyssaceae) has one to three carpels (Manchester et al., 1999; Takahashi et al., 2002). *Diplopanax* Hand.-Mazz. (Nyssaceae) is unilocular and *Mastixia* Blume has one (sometimes two) locules (Mai, 1993; Takahashi et al., 2002). Based on the current characters known for the Eden Main fruits, *Nyssa* or possibly *Camptotheca* are the most similar. Both of these extant taxa, however have germination valves that are short and only located near the apex of the fruit (Manchester et al., 1999; Takahashi et al., 2002); the length of the valves in the Eden Main fruits is currently unknown, but they appear to be elongate. All extant genera

except *Camptotheca* have longitudinal grooves (Takahashi et al., 2002). The Eden Main fruit appears to have ridges but needs further preparation to compare to known taxa.

Fossil taxa of Cornales comparable to the Eden Main fossil include *Hironia fusiformis* Takahashi Crane et. Manchester from the Coniacian of Japan, the oldest known member of the Cornales (Takahashi et al., 2002) and *Amersinia* Manchester, Crane et Goloveneva from the Paleocene of North America and eastern Asia (Manchester et al., 1999). *Hironia fusiformis* is a fusiform cornalean fruit with elongate germination valves, described from charcoalified and mummified/lignitized remains (Takahashi et al., 2002). Like the Eden Main fruits, *Hironia* has a fibrous endocarp and three to four locules. In *Hironia* the outer layers of the endocarp are composed of sclereids. The Eden Main fruits need to be peeled further to determine the exact nature of the endocarp layers. *Hironia* is reported to have tabular cells that line the locule (Takahashi et al., 2002), these may be similar to those cells seen in the locules of some of the Eden Main fossils (Plate 22, Fig. 5). Similar cells are also known from *Amersinia* (Manchester et al., 1999). *Amersinia* has obtrullate (trowel-shaped) fruits, a fleshy mesocarp and three (rarely up to four) locules. Once the shape of the Eden Main fruits, the complete length of the germination valves, and location of the vascular bundles are known, further comparisons to both extant and extinct taxa may be possible. With the information currently available, it appears that this fruit may be similar to *Hironia*.

Three-loculed cornalean fruit with fleshy mesocarp

(Plate 25, Figs. 4-5)

Description: One specimen of a three-loculed drupaceous fruit 3 mm in diameter, with parenchymatous mesocarp and sclerotic endocarp is known. The mesocarp is composed

of cells circular to oval in cross section, up to 230 μm in diameter and elongate parenchyma cells up to 70 μm in diameter and 240 μm long (Plate 25, Fig. 2-5). At the inside of the mesocarp and outside of the endocarp are *ca* nine poorly preserved fibrous bundles up to 0.3 mm in diameter. The endocarp is sclerotic and up to 0.24 mm thick. The inner endocarp has *ca* three layers of horizontally aligned fibers 12 μm in diameter and at least 150 μm long (Plate 25, Fig. 5). The outer endocarp is composed of sclereids up to 30 μm in diameter (Plate 25, Fig. 5). Locules appear to be empty, with no germination valves visible.

Occurrence: Eden Quarry: P144604 A, and B top.

Discussion: Fruits with a parenchymatous mesocarp containing fibrous bundles, and a sclerotic endocarp with three locules are similar to fruits that have been described in the Cornaceae (Manchester et al., 1999). *Amersinia* is a Paleocene genus that has been compared to extant *Davidia* or *Camptotheca* (see above) and has a parenchymatous mesocarp with a ring of fibrous bundles just outside of the endocarp (Manchester et al., 1999). Like the Eden Main fruits, the inner endocarp of *Amersinia* is composed of horizontally aligned fibers and the outer endocarp of sclereids. The germination valves in *Amersinia* only occur in the upper 1/4 of the fruit. As valves are not visible in the Eden Main fruit it suggests that this may be a basal section and that the valves were not elongate, unlike those described in the previous fruit.

?Two-loculed fruit

(Plate 26, Figs. 1-2)

Description: One specimen of a drupaceous fruit in longitudinal section with a sclerotic endocarp and at least two locules (Plate 26, Fig. 1) has been identified. The fruit is 1.6

mm wide and 1.7 mm long. The outer edge of the abraded endocarp is composed of one to two layers of cells up to 30 µm in diameter. Outside this layer is an amorphous material that probably represents the degraded mesocarp (Plate 26, Figs. 1-2). The inner endocarp is composed of thick-walled sclereids up to 90 µm in diameter (Plate 26, Fig. 2). Two locules are visible that are up to 1.2 mm long and 0.4 mm wide (Plate 26, Figs. 1-2). Locules are lined with square to rectangular cells up to 40 µm in diameter (Plate 26, Fig. 2). Material in the locules probably represents seed remains (Plate 26, Fig. 2).

Occurrence: Eden Main 2nd Ditch: P14467 A #1.

Discussion: This drupaceous fruit could represent a longitudinal section through a cornalean fruit. The determination of the presence of germination valves, number of locules, a single seed per locule and apical placentation would allow the placement of this taxon into the Cornaceae.

Order: ?Ericales

Three-loculed fruit with spiny/ridged seeds

(Plate 27, Figs. 1-3)

Description: One specimen of a syncarpous three-loculed fruit is known that is circular in cross section, and *ca* 4 mm long (*ca* 170 peels x 25 µm per peel) and 1.8 mm wide (Plate 27, Fig. 1). The fruit is surrounded by fleshy tepals; epidermis on the tepals consists of cells that are rectangular in cross section 36 µm long and 15 µm wide (Plate 27, Fig. 2). Tepals are composed of thick-walled cells, that are round to oval in cross section, 45-120 µm at their widest diameter (Plate 27, Fig. 2). Interspersed amongst the thick-walled cells are individual cells or patches of thin-walled cells that are similar in size to the thick-walled cells (Plate 27, Fig. 2). The base of the tepals are fused and surround the basal half

of the fruit, midway towards the apex, the tips of the tepals are free and form at least three (probably five) imbricating leaf like sections (Plate 27, Fig. 1). In apical sections, the tepals are not present/preserved. Mesocarp is not preserved. The endocarp is composed of sclereids, 24-48 μm in diameter (Plate 27, Figs. 1, 3). Thin lines in the walls of the septum suggest that this fruit dehisced via septicidal dehiscence (Plate 27, Fig. 1). Within each locule are multiple seeds that are 0.45 mm in diameter and ornamented with ridges or spines (Plate 27, Fig. 3). The placentation in the fruit is difficult to determine.

Occurrence: The Ditch: P14492 C bot.

Discussion: This fruit has three locules, each with multiple ridged/spiny seeds and septicidal dehiscence. Fruits with several locules (two to ten carpels) with septicidal or loculicidal dehiscence are found in the Ericales (Cronquist, 1981; Keller et al., 1996; Stevens, 2001 onwards), an order that extends back to at least the Turonian (Nixon and Crepet, 1993). Fossil fruits with ericalean affinities with ridged seeds that may be comparable to those in the Eden Main fruits have been described from the Cretaceous (e.g. Keller et al., 1996; Takahashi et al., 1999b; Schönenberger and Friis, 2001; E.M. Friis, personal communication, 2006). Like the Eden Main fruit, many Cretaceous flowers/fruits of ericalean affinity have three locules (see Schönenberger and Friis, 2001 for review) A fruit/flower type with probable ericalean affinities from the Coniacian Kamikitaba Locality has five thick tepals that surround the fruit (Takahashi et al., 1999b). These tepals may be similar to the tube-like perianth parts that surround the Eden Main fruit. This fruit will have to be throughly studied and reconstructed three dimensionally to properly compare it to extant and extinct taxa.

Multi-loculed ?ericalean fruit

(Plate 27, Figs. 4-7)

Description: A single specimen of a multilocular fruit with spiny seeds (Plate 27, Fig. 4) is known. The fruit is circular in oblique longitudinal section, 7.0 mm in diameter. At the base of the fruit is a pedicel with a parenchymatous cortex with cells up to 60 μm in diameter (Plate 27, Figs. 4, 6, 7). When seen in cross section the pedicel has small amount of secondary xylem (Plate 27, Fig. 6). At the base of the fruit is a fleshy cupule composed of cells similar to those of the pedicel (Plate 27, Figs. 4, 7). Between the cupule and the fruit, a small amount of crushed parenchymatous perianth is present. The mesocarp is either thin or degraded and only a thin black outer layer remains (Plate 27, Fig. 7). The endocarp is sclerotic (Plate 27, Figs. 4, 7), 0.2 mm in diameter, composed of cells up to 30 μm in diameter with wavy margins. There are at least three locules in the fruit, that appear to have had septicidal dehiscence (Plate 27, Fig. 4). Each locule bears numerous ridged or spiny seeds to 1.0 mm long and 0.4 mm wide that are attached to the axis of the fruit by a placenta composed of parenchymatous cells, round in transverse section, up to 60 μm in diameter (Plate 27, Fig. 5).

Occurrence: Eden Quarry: P14489 B top.

Discussion: This fruit is at least superficially similar to unknown fruit 6. However, this fruit is much larger, and lacks the covering tepals. The fruit will have to be thoroughly peeled to determine the number of locules present, but it may also have an ericalean affinity.

?Ericalean fruit w/spiny seeds

(Plate 28, Figs. 1-2)

Description: A single specimen of a fruit seen in longitudinal section 3.4 mm long and 1.5 mm in diameter, with spiny/ridged seeds (Plate 28, Fig. 1.) Has been identified from Eden Main. The base of the fruit is fleshy with parenchymatous cells, up to 48 µm in diameter (Plate 28, Fig. 1). Remnants of the perianth overarch the fruit (Plate 28, Fig. 1). Inside the fruit are spiny or ridged seeds up to 1.0 mm long and 0.30 mm wide (Plate 28, Fig. 2)

Occurrence: 2nd Ditch: P14468 E top.

Discussion: The histology of this fruit is similar to unknown fruit 7, and may be a similar fruit at a younger stage of development, or a smaller fruit. This specimen will have to be peeled further to determine the nature of the fruit layers, number of locules, placentation, etc..

Incertae sedis

Unknown fruit 1

(Plate 29, Figs. 1-2)

Description: One specimen of a single-loculed ridged fruit (Plate 29, Fig. 1) has been found. The fruit appears to have small ridges in section view, and has two large ridges or wings (Plate 29, Fig. 1). The fruit is 8.5 mm from the tip of one large ridge (or wing) to the other (Plate 29, Fig. 1). The mesocarp is composed of thick-walled parenchyma, up to 65 µm in diameter that is interspersed with larger thick-walled cells, up to 120 µm in diameter and *ca* 420 µm long (Plate 29, Fig. 2). The mesocarp in each of the large ridges has a suture or germination valve that is also present in the endocarp (Plate 29, Figs. 1-2).

The endocarp is up to 0.2 mm in diameter and is composed of sclereids up to 60 µm in diameter (Plate 29, Fig. 2).

Occurrence: Eden Quarry: P15037 A.

Unknown fruit 2

(Plate 29, Figs. 3-4)

Description: One specimen of a two loculed fruit with a central vascular bundle (Plate 29, Fig. 3) is known. The fruit is *ca* oval in transverse section (Plate 29, Fig. 3), 1.6 mm long and 1.0 mm wide. The mesocarp is composed of parenchymatous cells up to 54 µm in diameter. Between the locules at the center of the mesocarp is a poorly preserved vascular bundle, 120 µm in diameter (Plate 29, Fig. 3). There is a thin sclerotic endocarp with cells up to 30 µm in diameter (Plate 29, Figs. 3, 4). Locules are lined with a single layer of rectangular cells, 30 µm long and 21 µm wide (Plate 29, Fig. 4). Inside of one locule is a patch of interdigitate cells, up to 24 µm in diameter each, that are probably part of the seed coat (Plate 29, Fig. 4).

Occurrence: Eden Quarry: P14347 E bot.

Unknown fruit 3

(Plate 29, Fig. 5)

Description: Three examples are known of a triangular three-loculed fruit are known from the Eden Main localities (Plate 29, Fig. 5). Fruits are up to 2.5 mm in diameter at their widest point. The only fruit layer present is endocarp, 0.2 mm thick, that is composed of sclereids, up to 36 µm in diameter (Plate 29, Fig. 5). The locules are empty. Broken locule walls suggest this fruit had loculicidal dehiscence (Plate 29, Fig. 5).

Vascular bundles have not been observed, but poorly preserved tissue suggests there may have been a central axillary bundle present in these fruits.

Occurrence: Eden Quarry: P14345 E top; P14347 C top; P14462 F top.

Unknown Fruit 4

(Plate 30, Figs. 1-2)

Description: A Drupaceous three-loculed fruit is recognized. The fruit is ~ triangular in cross section and is 1.2 mm in diameter (Plate 30, Fig. 1). The endocarp is ca 0.2 mm thick and is composed of sclerenchyma cells, up to 36 µm in diameter (Plate 30, Fig.1). Locules are lined by cells that are square-shaped in cross section, up to 30 µm in diameter (Plate 30, Fig. 2).

Occurrence: Eden Quarry: P14320 B bot.

Unknown fruit 5

(Plate 30, Figs. 3-4)

Description: Two fusainized specimens of a three-loculed fruit with contents, triangular in cross section, are known from the Eden Main localities (Plate 30, Fig. 3). Fruits are up to 0.8 mm in diameter, and are surrounded by three sepals (Plate 30, Fig. 3). The pericarp is poorly preserved with most of the tissue being amorphous, but a few cells remain that are up to 35 µm in diameter (Plate 30, Fig. 4). Locules are up to 0.6 mm in diameter. Often seeds are present that fill the locule, composed of thin-walled cells up to 42 µm in diameter (Plate 30, Fig. 4). Seeds appear to be empty in section view (Plate 30, Fig. 4).

Occurrence: Eden Ditch: P13527 C bot; P14492 C bot.

Unknown fruit 6

(Plate 30, Figs. 5-6)

Description: At least three specimens of a three-loculed fruit with a fleshy mesocarp and sclerotic endocarp (Plate 30, Fig. 5) are known. The fruits are circular in section view, up to 2.4 mm in diameter. The mesocarp is 0.3 mm thick, is parenchymatous with cells up to 60 μm in diameter (Plate 30, Figs. 5-6). A dark layer external to the mesocarp may represent the remains of the exocarp (Plate 30, Fig. 6). The endocarp is 0.23 mm thick and composed of sclereids up to 60 μm in diameter (Plate 30, Fig. 5). Each locule contains a suture that extends from the locule to the edge of the endocarp (Plate 30, Fig. 5, arrow). Locules are lined with thick-walled cells that are square to rectangular in section, up to 45 μm in diameter (Plate 30, Fig. 6). Poorly preserved contents within the locules may represent the remains of seeds (Plate 30, Fig. 5).

Occurrence: Eden Quarry; Eden Main 2nd Ditch: P14338 D top; P14467 B top, P14468 C bot.

Unknown fruit 7

(Plate 31, Fig. 1)

Description: A single specimen of a ridged five-locular fruit, 1.0 mm in diameter (Plate 31, Fig. 1) has been identified. The fruit is not well preserved and composition of the pericarp is unknown. Poorly preserved contents in some of the locules may be the remains of seeds (Plate 31, Fig. 1).

Occurrence: Eden Quarry: P14460 G top.

Unknown flower

(Plate 31, Fig. 2)

Description: A single specimen of a flower, 1.0 mm in diameter, with a ridged five-loculed gynoecium is known (Plate 31, Fig. 2) is recognized. The outer perianth consists of at least two whorls but is poorly preserved (Plate 31, Fig. 2). Three introrse stamens are preserved, but there were likely at least four (or five) present. Pollen has not been found (Plate 31, Fig. 2). The gynoecium is 0.45 mm in diameter, and cells are poorly preserved in all tissues (Plate 31, Fig. 2).

Occurrence: Eden Quarry: PT4320 E bot.

Discussion: The affinities of this flower are currently unknown. However, the gynoecium contains five locules and is ridged much like unknown fruit 7.

Unknown fruit 8

(Plate 31, Figs. 3-5)

Description: Seven specimens of fruits, up to 3.2 mm in diameter, that are circular in cross section and have six locules are known from the Eden Main localities (Plate 31, Fig. 3). The outer layer of mesocarp is up to 0.6 mm thick and composed of thick-walled parenchyma cells (Plate 31, Figs. 3, 4, 5). The cells are radially elongate and measure up to 6 μm in wide and 120 μm long. The primary walls of the cells are thickened and are covered with numerous pits, *ca* 3 μm in diameter (Plate 31, Fig. 5). The inner fruit wall is composed of cells that are circular in cross section and thick-walled. Cells in this layer are up to 45 μm in diameter and may bear pits similar to those seen in the outer fruit wall (Plate 31, Fig. 4). Locules are lined with cells that are rectangular, up to 39 μm wide and 60 μm long (Plate 31, Fig. 4). Axially elongate, narrow cells in the mesocarp that appear

to extend from the locules, and the presence of a few fruits with broken locules in the collection, suggest that this fruit had loculicidal dehiscence (Plate 31, Fig 4.) . Some locules contain the remains of seeds that fill the locule (Plate 31, Fig. 4).

Occurrence: Eden Quarry; the Ditch; Eden 2nd Ditch: P14319 B top; P14338 D top; P14464 E top; P14467 B bot; P14531 D bot; P14596 C top; P14468 C bot.

Discussion: Fossils with similar anatomy to the Eden Main fruit are *Wetherellia* Bowerbank, and *Tiffneycarpa* Manchester from the Eocene of England and North America, and *Palaeowetherellia* Chandler possibly from Late Cretaceous of Eygpt and Eocene deposits of England (Reid and Chandler, 1933; Chandler, 1954; Mazer and Tiffney, 1982; Manchester, 1994).

Wetherellia fruits are 12-24 mm in diameter, with two to eight carpels, and generally have a solid axis. *Wetherellia* fruits are circular in cross section, ridged, with a spongy to woody mesocarp, and are thought to have had both septicidal and loculicidal dehiscence. They have a system of elongate cells that have been interpreted as secretory structures (Mazer and Tiffney, 1982) or fibre bundles (Manchester, 1994) that may extend from the axis to the periphery of the fruit.

Paleowetherellia fruits are similar in size and histology to *Wetherellia* (Reid and Chandler, 1933; Chandler, 1954; Mazer and Tiffney, 1982). However, *Palaeowetherellia* can have six to twelve carpels, a hollow central axis, and usually has loculicidal dehiscence.

The Eden Main fruit is much smaller than either of these genera, has only been observed to have six locules, and lacks ridges. The Eden fruit appears to have had loculicidal dehiscence and a solid axis, although tissues have often degraded leaving a

hollow zone with scattered cellular remains at the center of the fruit. Secretory structures/fibre bundles are not known in the Eden Main fruit.

Tiffneycarpa is known from one specimen. It is a ridged fruit that is circular in cross section that is 9.5 mm in diameter and has ten carpels and eight locules (Manchester, 1994). This fruit has only been observed to have loculicidal dehiscence. *Tiffneycarpa is* much larger, ridged and has many more locules than the Eden main fruit.

The affinities of *Wetherellia* and *Palaeowetherellia* are unknown but affinities with Euphorbiaceae, Linaceae, Meliaceae as well as other families have been suggested (Reid and Chandler, 1933, Chandler, 1964; Mazer, 1982). The affinities of *Tiffneycarpa* are unknown. The Eden Main fruit will have to be throughly peeled and reconstructed to fully compare it to similar fossil and extant taxa.

Unknown fruit 9

(Plate 32, Figs. 1-5)

Description: Two fruit specimens, circular to oval in section view with numerous seeds (Plate 32, Figs. 1, 2) are known from Eden Main. Fruits measure up to 5.4 mm in diameter. Cells of the outermost layer in the fruits may have been parenchymatous and are not well preserved. Within this outer layer (mesocarp) are bundles that are circular in section view, up to 40 µm in diameter (Plate 32, Figs. 2, 5). These bundles are composed of elongate fibers, 9.0 µm in diameter. The internal structure of the fruit has a complicated arrangement that is not currently well understood. There is a layer (?endocarp) of parenchymatous tissue that lies inside of the fibrous bundles and is not well preserved and is 0.24 mm thick (Plate 32, Figs. 1, 4). This layer forms partitions, also composed of parenchymatous tissue with cells that are rectangular in section view, up

to 30 μm wide and 120 μm long, that traverse the inside of the fruit (Plate 32, Fig. 1). These partitions can contain tracheary elements that are poorly preserved but appear to have scalariform thickenings (Plate 32, Fig. 3). Among the partitions are elongate thin seeds. Seeds are narrow, elongate, at least 1.5 mm long and 184 μm wide (Plate 32, Figs. 4, 5). Seeds are not well preserved and often appear compressed and have a seed coat composed of square to rectangular cells, up to 12 μm in diameter (Plate 32, Fig. 5). Inside this layer some seeds show ovoid cells that may measure up to 60 μm in diameter (Plate 32, Fig. 5).

Occurrence: Eden Quarry; unknown locality: P14489 C bot; P14546 G.

Unknown fruit 10

(Plate 33, Figs. 1-3)

Description: Many specimens of unknown ridged fruits or seeds are known from the Eden Main localities. Fragments of ridged fruits or seeds are common in concretions. A few whole specimens are known (Plate 33, Fig. 1). They measure up to 6 mm long and 2 mm wide. An outer layer of dark material is seen in the grooves between ridges in the endocarp and probably represents a fleshy layer of pericarp that is degraded; but a few cells are present that are circular in section view, and 24 μm in diameter (Plate 33, Fig. 2). The endocarp is 0.8 mm thick, ridged and composed of two layers (Plate 33, Figs. 1-2). The outer layer is composed of 2-3 layers of sclereids that appear more or less circular in section view, up to 60 μm in diameter. The remainder of the endocarp is composed of intertwined fibers that measure *ca* 36 μm in diameter. Poorly preserved material inside of the endocarp probably represents the remains of a seed (Plate 33, Fig. 1).

A ridged fruit or seed has also been found on the external surface of a calcium carbonate concretion (Plate 33, Fig. 3). The specimen is 4.5 mm in diameter and has a circular mark on its apex that probably represents the vascular bundle (Plate 33, Fig. 3). Only the parts of the fruit that lie outside the concretion have been peeled, and internal anatomy is not well preserved. It is very probable that the ridged fruits/seeds found at the localities represent several different taxa.

Occurrence: Known from all localities. Figured specimens: Eden Quarry; 2nd Ditch: P14332 A; P14468 F bot.

Unknown fruit 11

(Plate 34, Fig. 1)

Description: Two specimens of two-winged fruits, 3.7 mm long and 0.8 mm wide are known from the Eden Main localities (Plate 34, Fig. 1). Wings are composed of parenchyma cells that are circular in section view, up to 42 µm in diameter (Plate 34, Fig. 1). At the center of each wing is a dark line that extends from the endocarp to the tip of the wings that may represent a line of dehiscence (Plate 34, Fig. 1). The endocarp is thin and composed of *ca*four layers of thick-walled cells (Plate 34, Fig. 1) that are circular in section view, up to 30 µm in diameter.

Occurrence: Eden Ditch 2nd Ditch: P13527 H; P14468 E top.

Unknown fruit 12, heart-shaped mericarps

(Plate 34, Figs. 2-5; Plate 35, Figs. 1-3)

Description: At least 30 specimens of two-winged heart-shaped fruits are known from the Eden Main localities, and are the most abundant recognized angiosperm fossil known there (Plate 34, Fig. 2). Fruits are *ca* 1.2 mm in diameter and 1.5 mm long. The exocarp

consists of tangentially elongate cells, up to 84 µm in tangential and 48 µm in radial diameter (Plate 34, Fig. 3). The mesocarp is composed of radially elongate parenchyma cells, up to 180 µm long and 120 µm wide and forms two wings (Plate 34, Figs. 2-5). When reconstructed in three dimensions, the wings are seen to be lobe-shaped (Plate 35, Figs. 1-3). The endocarp is composed of thick-walled fibers that measure up to 12 µm wide and at least 75 µm wide (Plate 34, Fig. 4). Each fruit contains a single seed that is 0.5 mm long and 0.3 mm wide (Plate 34, Figs. 2, 4, 5; Plate 35, Figs. 1-2).

One specimen of a schizocarpic fruit has been found that was separating into six heart-shaped mericarps when it was fossilized (Plate 34, Fig. 5). The schizocarp is 2.5 mm in diameter and appears to have been disc-shaped.

Occurrence: Known from all localities except Eden Creek. Figured specimens: Eden Quarry; The Ditch: P14355 C top; P14605 B top.

Discussion: Heart-shaped mericarps are the most common angiosperm fossil found at the Eden Main localities. The affinities of these fruits are unknown.

Conclusions: Seed plant organs are very common in concretions collected from the Eden Main fossil localities. Gymnosperms are represented by a cycadeoid stem, and organs of Pinaceae, Cupressaceae and possible Araucariaceae. Conifers leaves (Cupressaceae) are the most common recognizable fossil found. Angiosperms are the most diverse group found and are represented by flowers, fruits, and wood, some of which are assignable to the families Lauraceae, Platanaceae, Nyssaceae, and possibly the order Ericales. Several other angiosperm organs remain as unclassifiable morphotaxa, revealing the need for future work.

Chapter 5

Conclusions

This work documents the known diversity at the Coniacian Eden Main fossil localities located on Vancouver Island. Taxa are represented by twelve types of seedless land plants (Chapters 2 and 3), at least seven different gymnosperms and at least twenty-five angiosperms (Chapter 4). There are also a variety of unidentified organs and numerous leaves that probably belong to ferns, gymnosperms, and angiosperms, but these have not yet been assigned to known taxa.

The plant diversity of the Eden Main localities is comparable to that of other Turonian to Campanian floras. According to Crane (1987), 10% of species found in Turonian-Campanian megafossil floras are pteridophyte species, 10% are conifers, and 70% are angiosperms. These percentages change according to paleolatitude (Crane, 1987). Though the full diversity of the Eden Main localities is not yet recognized, the diversity of the flora, as currently known, may be broken down into three major groups: pteridophyte taxa 25% (of known diversity), gymnosperms (one cycadeoid and six conifer organ types) 16% and angiosperms 57%. The high diversity of ferns may be due to sorting prior to deposition, as various plant parts become waterlogged at different rates (Nichols et al., 2000). Another possibility is that these ferns were colonizers of disturbed habitats which were easily transported into a marine environment (e.g., by storms) and are therefore, over-represented in the fossil assemblage. Conifer diversity will increase if the various cupressaceous organs are shown to come from different taxa.

Seedless taxa

Mosses are rare in the fossil record due to their small size and delicate tissues. Moss gametophytes are not common at the localities, but when found they are generally not greatly abraded and still display minute leaves arranged around the gametophyte axis. The fossil mosses from Eden Main are the only permineralized mosses known from the Late Cretaceous and are older then the Santonian and Campanian fusainized taxa described from Georgia, U.S.A. (Herendeen et al, 1999; Konopka, 1997, 1998). Lycopod fossils are not currently known from the localities. Lycopod fossils are absent at many localities of similar age (e.g., Nishida, 1991), or only known from spores (Takahashi et al., 1999b). Fossils of the Equisetales are unknown from the Eden Main localities and are not common at other similar aged localities (see Nishida, 1991).

The Eden Main localities contain plant organs assignable to many extant fern families including; Gleicheniaceae, Schizaeaceae, Cyatheaceae, and some may represent the oldest known permineralized examples of Dryopteridaceae/Blechnaceae. Most of these taxa are represented by vegetative organs except for the fertile pinnules of *Paralygodium meckertii* sp. nov. which contain numerous trilete spores. Never-the-less, some of the fossils show diagnostic anatomical characters found only in a few families of ferns.

Fern organs are common in concretions from the Eden Main localities, especially gleicheniaceous rachides. Some of the fern families present (Gleicheniaceae, Schizaeaceae) are families that had originated during the second major filicalean fern radiation that probably had begun by the Permian (Lovis, 1977; Crane, 1987; Rothwell, 1987). Extant relatives of these ferns are often found growing in dry, open environments, and are colonizers of disturbed habitats (e.g., Crane, 1987; Kramer, 1990a, 1990c,

1990d). As fusian is abundant at the localities, it is possible that these ferns were colonizing areas that had been disturbed by fire. Other fern remains at Eden Main probably represent more derived fern families (e.g., Dryopteridaceae, Blechnaceae) that are thought to have arisen during the Cretaceous to Paleogene as part of the third filicalean fern radiation (Lovis, 1977; Crane, 1987; Rothwell, 1987). This radiation may have been triggered by the creation of new complex habitats as dominant members of the flora were replaced with angiosperms (Lovis, 1977; Rothwell, 1987; Crane, 1987; Schneider et al., 2004). Many extant, derived ferns live in the understory of angiosperm forests or live in the canopy as epiphytes (e.g., Schneider et al., 2004). This intimate relationship between ferns and angiosperms was in its infancy during the Coniacian.

Gymnosperms

Gymnosperm fossils are common at the Eden Main localities with eight taxa currently recognized. So far, cycadeoids are known by a single stem. Cycadeoid fossils are known from numerous sites around the world spanning the Triassic to the Late Cretaceous (Stewart and Rothwell, 1993). Fossils of the cycadeoid genera *Cycadeoidea* Buckland, *Cycadeoidella* Ogura (e.g., Nishida, 1991) and, *Bucklandia* Presl. (Saiki and Yoshida, 1999) are known from permineralized stems from the Turonian to Maastrichtian of Hokkaido, Japan. Compression/impression fossils of *Zamites* Brongniart, a cycadeoid leaf, are known from the Nanaimo Group (Bell, 1957).

Pinus leaves occur at Eden Main, and pinaceous fossils are also known from other sites of similar age (Ogura, 1932a; Ueda and Nishida, 1982, Stockey and Nishida, 1986, Takahashi et al., 1999b). The three and five-needled pines found at Eden Main probably represent the genus *Pinus*, Section *Diploxylon* (Koehne, 1893; Shaw, 1914; Pilger, 1926)

or section *Pinus* (Critchfield and Little, 1966), and are distinct from all other Cretaceous pine leaves. The presence of Pinaceae is also corroborated by a pollen cone with in situ bisaccate pollen. This is the earliest permineralized pinaceous pollen cone known in the fossil record.

The most abundant fossils found at Eden Main are taxodiaceous leaves of Cupressaceae. Permineralized and fusainized wood, and a few pollen cones that are probably cupressaceous are also known. Cupressaceae are also common in other Cretaceous floras, and it is thought that they may have been restricted to swamps or upland stands as angiosperm forests began to dominate the landscape during the Late Cretaceous (Crane, 1987).

Angiosperms

Angiosperms are the most diverse group found at the Eden Main localities. Magnoliid angiosperms (Lauraceae), eudicots (Proteales), as well as core eudicots (Angiosperm Phylogeny Group, 2003) (?Saxifragales, Cornales, ?Ericales) have been found at the Eden Main localities as well as other localities of similar age (e.g., Bell, 1957; Nishida, 1991; Magallón-Puebla, 1997; Takahashi et al., 1999b, 2002; Craggs, 2005). Undoubtably, more angiosperm taxa will be recognized if the localities are studied in more detail. Given the antiquity of these fossils, many of them may be impossible to place within our concept of extant families.

The bisexual platanaceous fossils found at Eden Main support the theory that bisexual platanaceous flowers and/or inflorescences would be found in the fossil record (Mindell, 2006b). The bisexual flowers and winged-seeds provide morphological evidence for the mostly molecular based placement of the Platanaceae into the Proteales

(Hoot et al., 1999; Doyle and Endress, 2000; Angiosperm Phylogeny Group, 2003; Hilu et al., 2003).

The oldest known fossil assignable to Cornales is from the Coniacian of Japan (Takahashi et al., 2002). The Eden Main localities are about the same age as the Japanese localities, but Cornaceae is more diverse at Eden Main, as at least two fruit types are present. At least one of these taxa deserves designation as a new genus or species, but both need to be studied in further detail. The diversity at Eden Main indicates that by the Coniacian, Cornaceae were more geographically widespread and diversified than previously known. There are several angiosperm fossils at the Eden Main localities that are of unknown affinity. These taxa reveal the need for future work , on both the fossils themselves, and the anatomy of extant taxa. Despite their unknown systematic affinities, the fossil flowers, and fruits described in this thesis show a large range of morphological diversity. It is thought that the propagules of many Cretaceous angiosperms were dispersed by abiotic means (Tiffney, 1984, 2004). The presence of fleshy fruits, sclerotic, and wing-fruits at Eden Main suggests a variety of dispersal mechanisms were established in western North America by the Coniacian.

Climate, Fire, and Paleolatitude

Many of the identified fossil plants from the Eden Main localities have affinities with extant taxa currently found in tropical habitats (see Chapters 2-4). Of the fern, conifer and angiosperm families known from Eden Main, New Zealand and South America currently have the most numerous extant representatives (see Kramer, 1990a, 1990b, 1990d; Kramer et al., 1990, Stevens, 2001 onwards). Global temperatures during the Cretaceous were equable, warm, with little seasonal variability except for wet and dry

seasons (Hallam, 1985; Parrish, 1987). The entire globe is thought to have been especially warm from the Cenomanian to the Santonian, a time known as the "Cretaceous Thermal Maximum" (Bornemann et al., 2007). Compression/impression Coniacian leaf floras provide evidence of warm to moderate temperatures, even at high paleolatitudes (Herman and Spicer, 1997; Craggs, 2005; Eklund et al., 2004; Hayes et al., 2006). Prominent growth rings in conifer wood, as well as the presence of fusain at the Eden Main localities suggest that the plants preserved were probably also subject to wet and dry seasons.

It is impossible to know if the Eden Main fossils were deposited over a long time frame which would represent frequent wildfires, or if the fusain at the site represents a single wildfire event. Wildfire could have played a role in the transportation of plant material from land to the marine environment in which they were preserved. Current wildfires may burn away binding roots in the soil (see Scott, 2000; Martin, 2007) allowing soil erosion. Post fire rainfall may have dislodged large amounts of soil along with herbaceous plants, wood fragments, leaves, flowers, and fruits that were on the ground, allowing them to be transported out to sea before they were deposited at the Eden Main localities and fossilized.

The paleolatitude of some fossil localities of similar age to Eden Main are known, e.g., the Yezo Group in Hokkaido (35°N to 45°N) (Hoshi and Takashima, 1999; Kodama et al. 2002; Takashima et al., 2004). Once the composition of the Eden Main floral assemblage is throughly understood it may be possible to compare taxa to those of similar age from around the world. This may aid in the determination of the paleolatitude of the Eden Main localities at the time of deposition. Once a prediction of

paleolatitude can be made, it will contribute to the ongoing controversy of the position of Vancouver Island during the Cretaceous (e.g., Ward et al., 1997; Mahoney et al., 1999; Enkin et al., 2001; Kodama and Ward, 2001; BangYeon et al., 2004). It is thought that Vancouver Island could have had a paleolatitude of anywhere from 25°N (*ca* 3500 km south of the current position)(Ward et al., 1997) to 40°N (*ca* 1500 km south of the current position) (BangYeon et al., 2004). It is also possible that the island was even closer to its current position during the Cretaceous (Kodama and Ward, 2001).

Concluding Remarks

The Eden Main fossil localities contain a diverse assemblage of permineralized plant remains. These plants were transported into a marine environment, perhaps after wildfires had created soil conditions that were susceptible to erosion. Calcium carbonate concretions generally contain disarticulated plant remains which limits the potential of whole plant reconstructions. However, well-preserved bryophyte gametophytes, rhizomes, cones, leaves, flowers, fruits, and wood may allow for future taxonomic placement of many of the Eden Main fossil remains.

The diversity of the Eden Main localities reinforces hypotheses on the diversity of major plant groups during the Late Cretaceous, with early diverging leptosporangiate ferns becoming less common while derived ferns began to diversify (Lovis, 1977; Crane, 1987; Rothwell, 1987, Schneider et al., 2004). Diversity and ecological niches of angiosperms were expanding at the time plants found at the Eden Main localities were growing (e.g., Tiffney, 1984; Crane, 1987). There is no doubt that some stem group of angiosperms have gone extinct (e.g., Friis et al., 2005). The study of Early to Late Cretaceous angiosperms may reveal some of these stem groups and add to our knowledge

of extinct angiosperm anatomy and assist in the study of the origin of angiosperms. The numerous unidentified angiosperm organs at the Eden Main localities could therefore, provide important taxonomic information, once the flowering plant taxa are throughly understood.

This work is a preliminary survey of the Eden Main fossil localities. As I have repeated throughout this thesis, more research is required before the diversity and importance of the floral remains from the Eden Main fossil localities can be fully appreciated. Diversity documented, thus far, promises that future studies of the Eden Main localities will greatly add to our knowledge of Cretaceous climates, environments, as well as plants and their relationships with extant taxa.

Plate 1

Figs. 1-4. Dinoflagellate cysts and moss gametophyte.

Fig. 1. ?Dinoflagellate cysts in conifer seed. P14465 D top #2. X 333.

Fig. 2. ?Dinoflagellate cyst showing round central body and orthogonal processes. Note possible archeopyle (arrowhead). P14465 D top #2. X 721.

Fig. 3. Transverse section of moss gametophyte showing imbricate leaves. Note costa (C). P14347 C top #3f. X 130.

Fig. 4. Enlarged portion of Fig. 3, showing costa (C), unistratose leaf lamina (arrow). P14347 C top #3f. X 286.

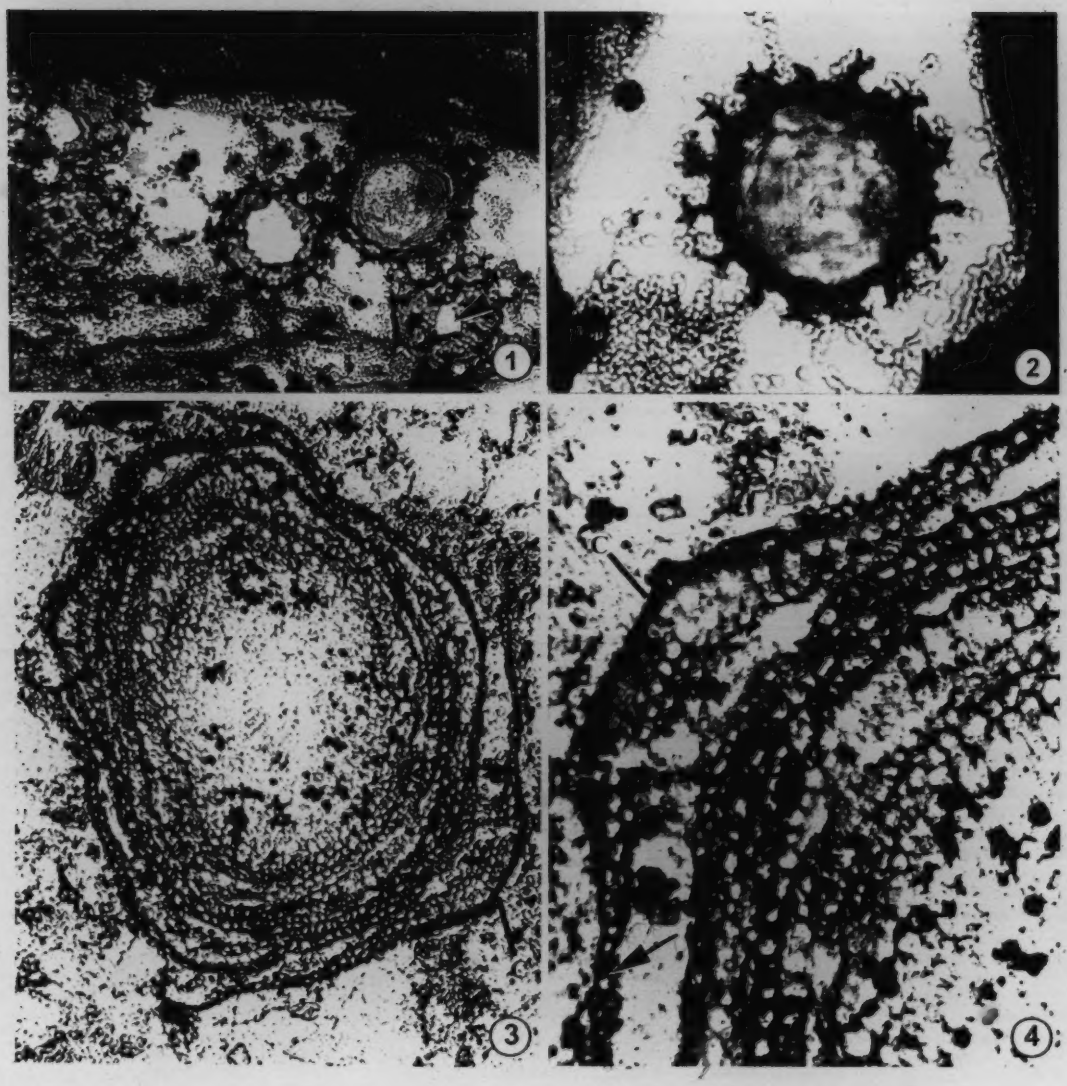
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Plate 2

Figs. 1-6. Gleicheniaceous rhizome, and frond segments.

Fig. 1. Transverse section of charcoalified rhizome with vitalized protostele showing xylem lobes (arrowheads); xylem intermixed with smaller parenchyma cells. P14399 C bot #25. X 39.

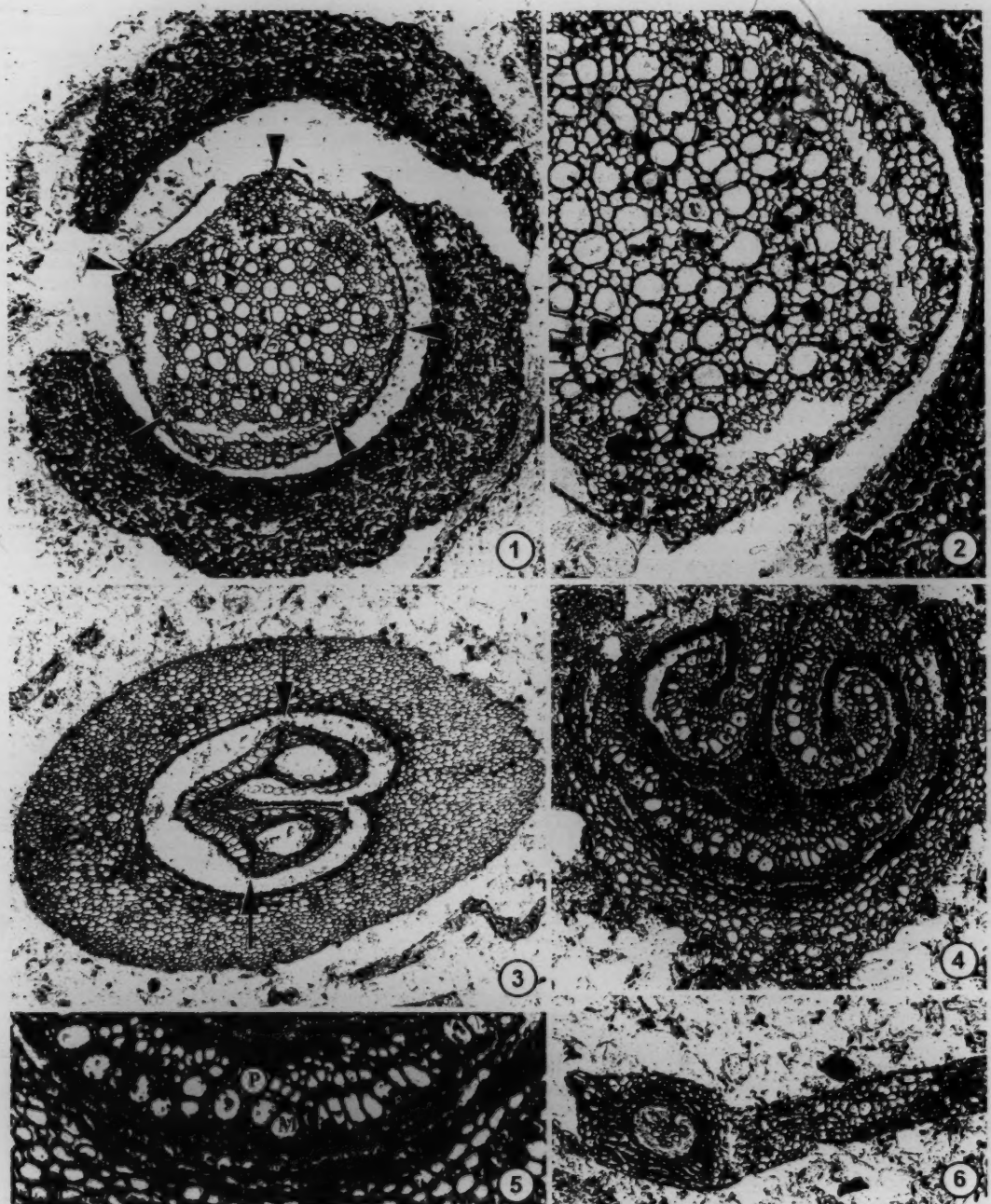
Fig. 2. Enlarged stele from Fig. 1. showing large tracheids surrounded by smaller parenchyma cells. Note xylem lobes and phloem (P). P14399 C bot #25 x 86.

Fig. 3. Transverse section of gleicheniaceous rachis showing constricted lateral xylem (arrows). P14592 A #3. X 22 .

Fig. 4. Transverse section of gleicheniaceous rachis showing sclerotic inner ground tissue xylem, and parenchymatous outer ground tissue. P14468 C bot #48b. X 42.

Fig. 5. Enlarged section of specimen in Fig. 2 with protoxylem (P), metaxylem (M). Note endarch primary xylem maturation. P14468 C bot #48b. X 116.

Fig. 6. Transverse section of gleicheniaceous pinnule showing midrib with attached laminar tissue. P14338 A #1. X 42.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P
M
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Plate 3

Figs. 1-4. Branching gleicheniaceous frond.

Fig. 1. Slightly oblique transverse section of branching gleicheniaceous frond segment showing abaxial arch of vascular tissue and adaxial rings of vascular tissue open on adaxial side (R). P14489 B top #63. X 28.

Fig. 2. Frond segment distal to Fig.1, showing three vascular bundles. P14489 B top #52. X 25.

Fig. 3. Rachis segment distal to Fig. 2, showing segment with three vascular bundles, at point of branching into three segments. P14489 B top #30. X 20.

Fig. 4. Three frond segments distal to Fig. 3. Two lateral segments and middle presumed dormant bud. Note degraded right lateral segment. P14489 B top #13. X 20.

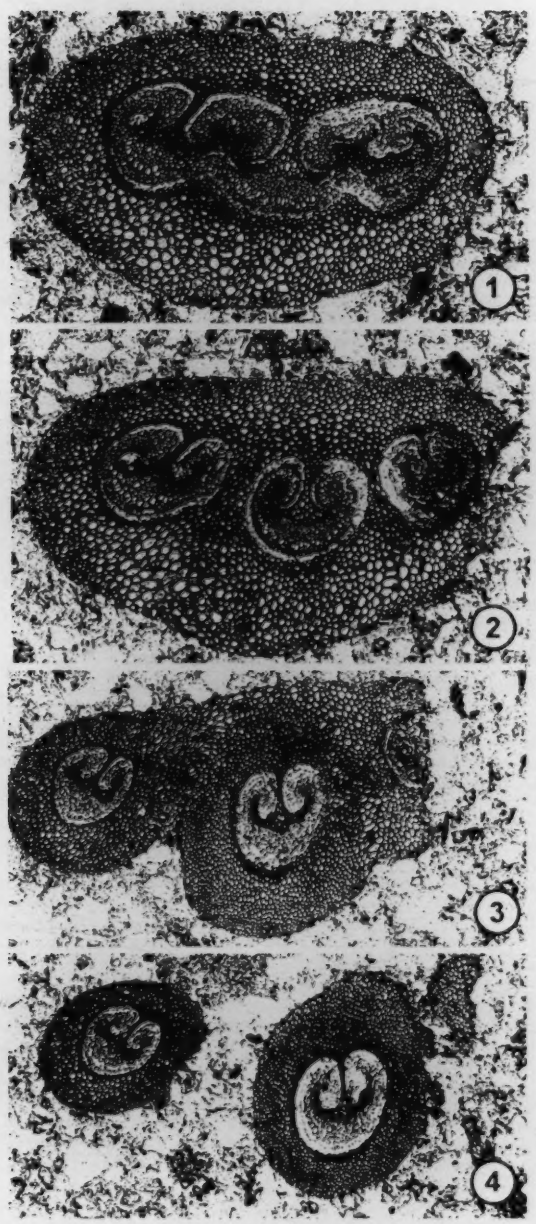
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Plate 4

Figures 1-5. Schizaeaceous and cyatheaceous fronds.

Fig. 1. Longitudinal section of *Paralygodium meckertii* fertile pinnule. Note sporangia and pinnule base (B). P14457 E top #5. X 28.

Fig. 2. Longitudinal section of schizaeaceous sporangia, showing smooth trilete spores and apical annuli (A). P14457 E top #5. X 150.

Fig. 3. Transverse section of cyatheaceous rachis (bottom) and diverging pinna (top). Note corrugated xylem of rachis and three-bundled pinna trace. P14504 C top #18. X 8.8.

Fig. 4. Abaxial strand of pinnule trace seen in Fig. 3, showing corrugated xylem, protoxylem lacunae (arrows) and mucilage cells (arrowheads). P14504 C top #18. X 33.

Fig. 5. Enlargement of rachis trace seen in Fig. 3, showing protoxylem lacunae (arrows), mucilage cells (arrowheads) and hypodermis (H). P14504 C top #18. X 40.

A
B
1
2
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4
5

Plate 5

Figs. 1-7. Transverse sections of various Eden Main fern rachides.

Fig.1. Dennstaedtiaceous rachis with sclerotic cortex and U-shaped vascular trace with incurved ends. P14338 C top #24b. X 53.

Fig. 2. Enlarged vascular trace from Fig. 1, showing enfolded abaxial hooks, and three visible protoxylem points (arrows). P14338 C top #24b. X 125.

Fig. 3. Dennstaedtiaceous rachis showing Ω-shaped vascular trace. P14320 G #1 x 16.

Fig. 4. ?Blechnaceous/dryopteridaceous rachis showing adaxial groove, two adaxial and one abaxial vascular bundles with sclerotic bundle sheaths. P13527 D bot d #2. X 37.

Fig. 5. ?Dryopteridaceous rachis with two hippocampiform bundles. P14511 B top #1. X 25.

Fig. 6. Unidentified rachis with two C-shaped vascular bundles. P14454 G top #1. X 26.

Fig. 7. Enlarged inner cortex of Fig. 6, showing phloem gap (P) and thick-walled cells with simple pits. P14454 G top #1. X 500.

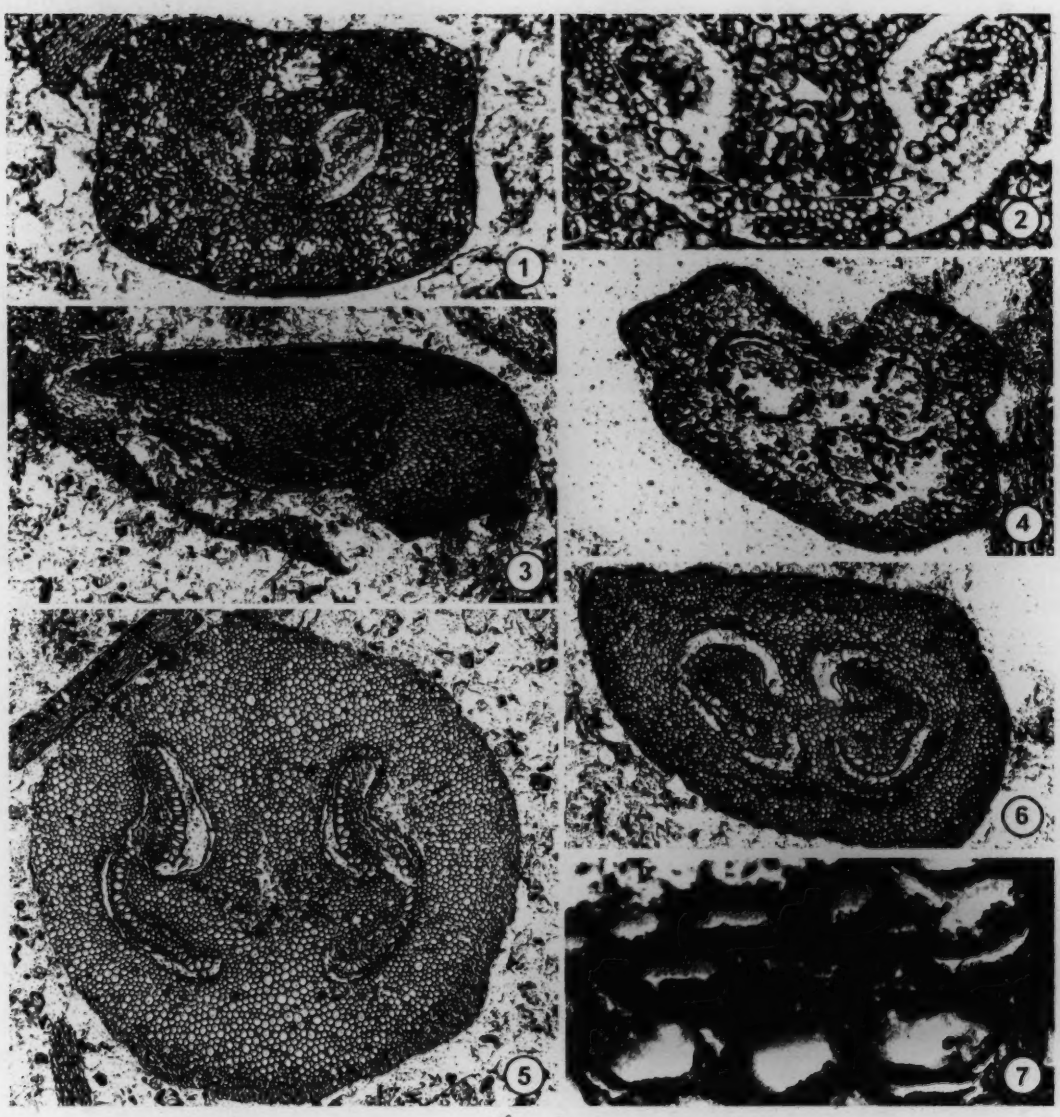
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Plate 6

Figs. 1-6. Exarch solenostelic fern rhizome *cf. Solenostelopteris*

Fig. 1. Transverse section of rhizome showing pith, xylem, phloem gap, endodermis (E), and root trace (RT). Note protoxylem groups (arrowheads) P14492 C bot #1. X 41.

Fig. 2. Transverse section of rhizome showing thin-walled cells of inner cortex, thick-walled cells of middle cortex and abraded outer cortex (OC). P14492 D #68. X 52.

Fig. 3. Section of rhizome showing metaxylem tracheids, protoxylem (arrowhead) and endodermis (E). P14492 D #68. X 208.

Fig. 4. Transverse section of rhizome showing two departing leaf traces (arrows). P14492 C bot #169. X 48.

Fig. 5. Transverse section of rhizome showing departing C-shaped leaf trace in cortex; protoxylem (arrow). Extension of rhizome pith on adaxial side of trace (P) and endodermis partially surrounds trace (E). P14492 C bot #146. X. 136.

Fig. 6. Diverging diarch root trace in cortex. P14492 C bot #9. X 227.

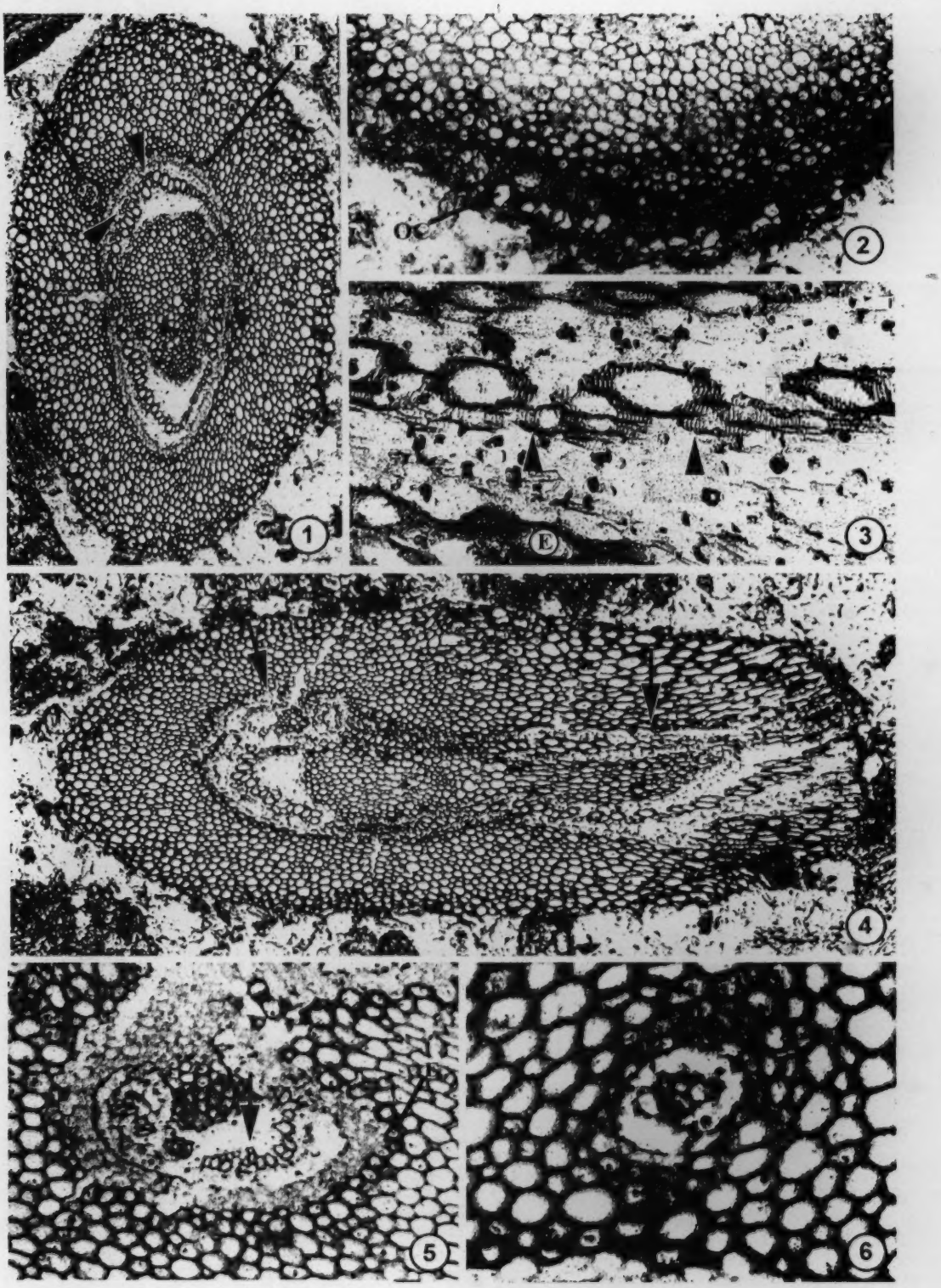
E
OC
E
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Plate 7

Figs. 1-4. Transverse section of unidentified solenostelic rhizome with three-bundled leaf trace.

Fig. 1. Rhizome showing outer cortex (OC), middle cortex (MC) and inner cortex (IC), amphiphloic solenostele, pith, and departing root trace (RT). P14579 B bot #20. X 44.

Fig. 2. Histology of rhizome, showing inner pith (IP), outer pith (OP), endodermis (E), pericycle (Pe), phloem (Ph), conjunctive parenchyma (CP), xylem (X), xylem parenchyma (*), inner cortex (IC). P14579 C top #76. X 285.

Fig. 3. Departing three bundled leaf trace. Note abaxial tip of reniform bundle (left) just separated, forming round abaxial bundle. P14579 C top # 70. X 75.

Fig. 4. Rhizome (top) and departing leaf. Note tissues of leaf similar to those of rhizome. P14579 B bot #1. X 28

Fig. 5. Diverging root trace between inner (top) and middle cortex. P14579 B bot #37. X 226.

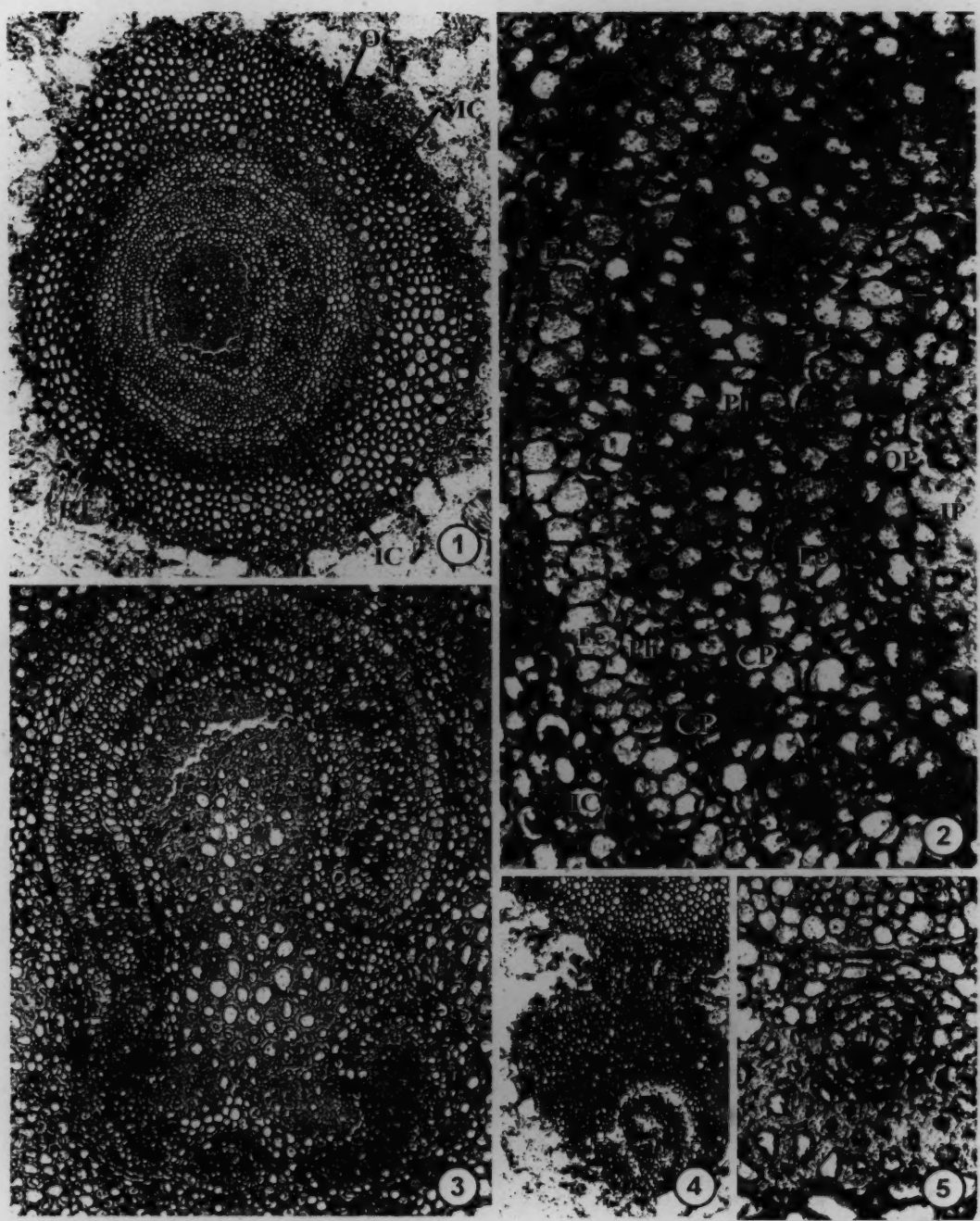
EC
MC
RL
IC
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Plate 8

Figs. 1-7. *Paralygodium meckertii*, general morphology.

Fig. 1. Fertile pinnule showing three major and four minor lobes in transverse section (arrows), pinnule base (at bottom) and numerous sporangia with spores. Holotype P14457 E top #9. X 39.

Fig. 2. Fertile pinnule showing three major and six minor lobes in transverse section (arrowheads) and numerous sporangia with spores. Paratype P14338 C top #3. X 40.

Fig. 3. Fertile pinnule showing thick adaxial cells, axially elongate abaxial cells of pinnule midrib, enrolled pinnule lobes, and numerous sporangia with spores. Paratype P14468 B top #7. X 32 .

Fig. 4. Fertile pinnule in paradermal section showing three major lobes in transverse section and axially elongate abaxial cells of pinnule midrib. Paratype P14334 D #1. X 25.

Fig. 5. Fertile pinnule in transverse section showing midrib (upper left), fragments of epidermis and numerous sporangia with spores. Paratype P14468 C bot #1, x 35.

Fig. 6. Adaxial laminar tissue showing elongate epidermal cells with sinuous margins. Paratype P14468 D bot #6. X 210.

Fig. 7. Abaxial epidermis, showing two stomata. Holotype P14457 E top #15. X 1575.

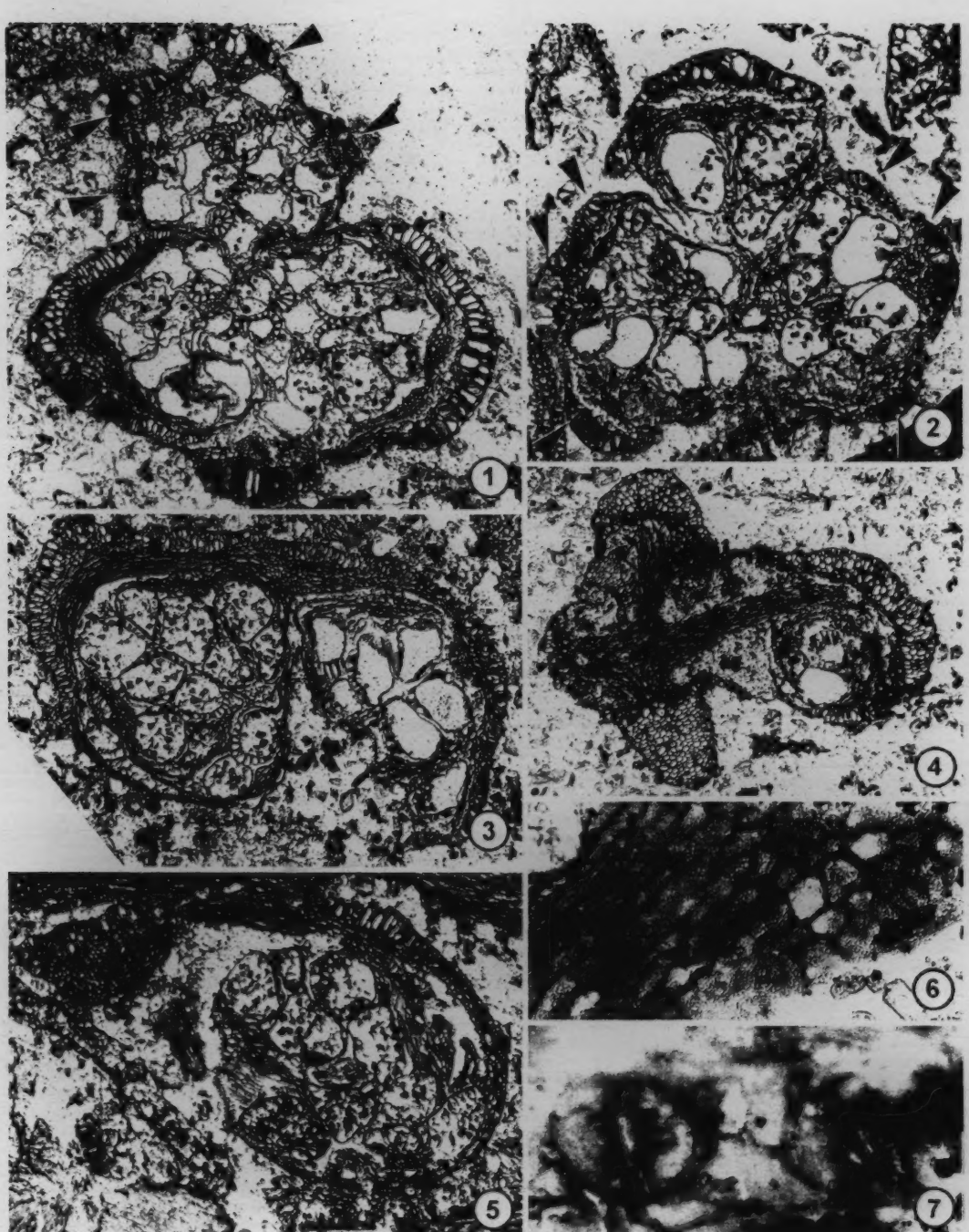
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Plate 9

Figs. 1-6. *Paralygodium meckertii*, general morphology and histology.

Fig.1. Major fertile pinnule lobe in transverse section showing tips of minor lobes in longitudinal section and numerous sporangia. Paratype P14468 D bot #5. X 34.

Fig. 2. Minor fertile pinnule lobe in transverse section showing terete vascular bundle, adaxial ridge of thick-walled cells and two sporangia. Holotype P14457 E top #4. X 276.

Fig. 3. Base of fertile pinnule in transverse section showing terete vascular bundle. Holotype P14457 E top #10. X 74.

Fig. 4. Tracheids in longitudinal section in fertile pinnule lobe, showing scalariform secondary wall thickenings. Paratype P14468 D bot #23. X 730.

Fig. 5. Section of fertile pinnule showing numerous paraphyses (arrows) and sporangia in various planes of section. Paratype P14468 D bot #23. X 131.

Fig. 6. Section of fertile pinnule showing sporangial attachment, apical annulus, and tip of minor lobe in longitudinal section. Note pyriform sporangial shape (lower right). Paratype P14468 D bot #24. X 140.

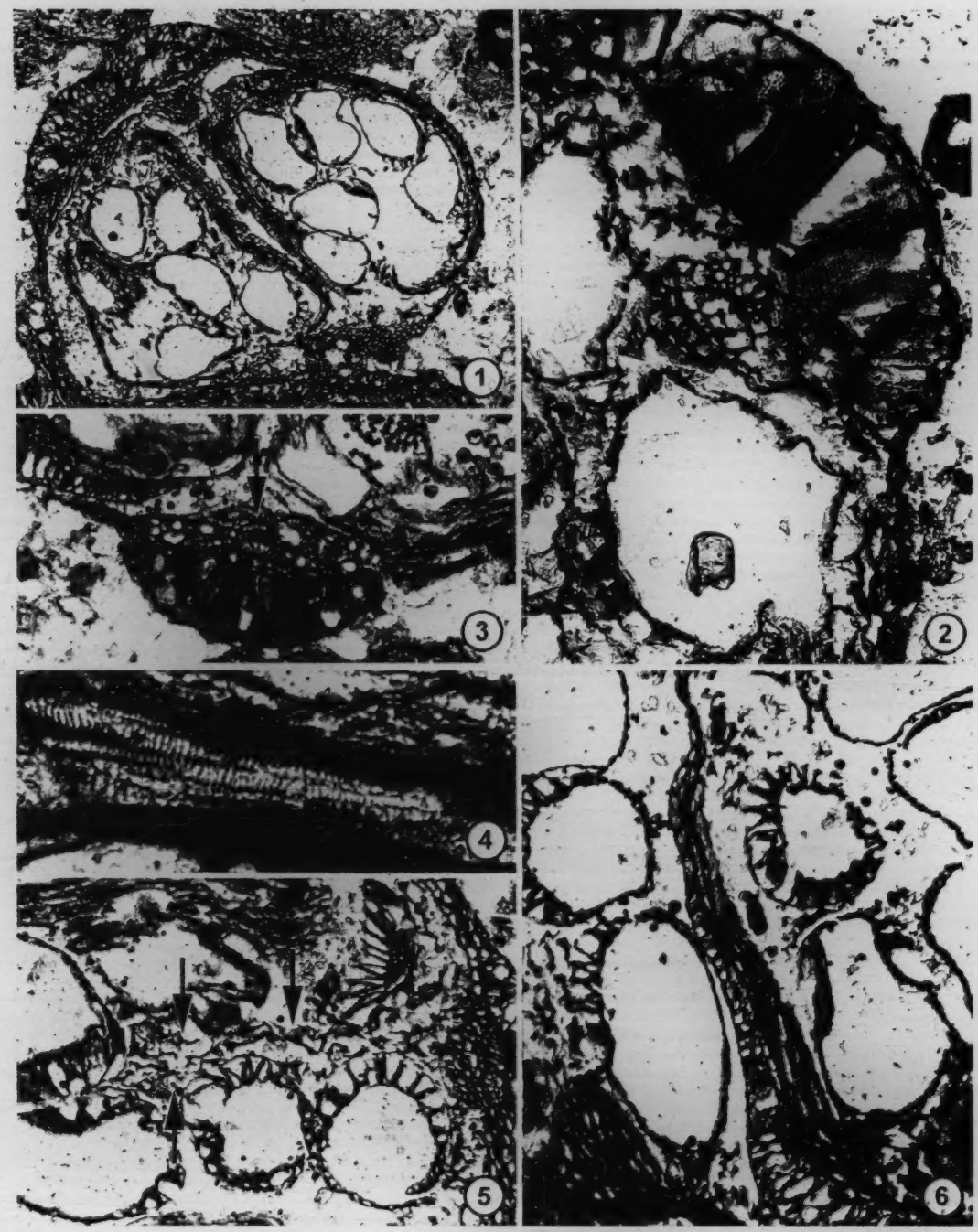
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Plate 10

Figs. 1-6. *Paralygodium meckertii*, spores.

Fig. 1. *In situ* spores shown in various orientations. P14457 E top #14. X 438.

Fig. 2. Spore, proximal view showing trilete suture (bottom), and other spores in various orientations. Holotype P14457 E top #3. X 750.

Fig. 3. SEM of spore group. Note small perforations or holes in spore wall. Holotype P14457 E top #11. X 759.

Fig. 4. SEM proximal view of spore showing trilete suture. Holotype P14457 E top #11. X 1849.

Fig. 5. SEM of spore wall in transverse section (center). Note lack of sculpturing. Holotype P14457 E top #6. X 24500.

Fig. 6. SEM of spore wall in transverse section near trilete suture, showing hole in exine. Holotype P14457 E top #6. X 13230.

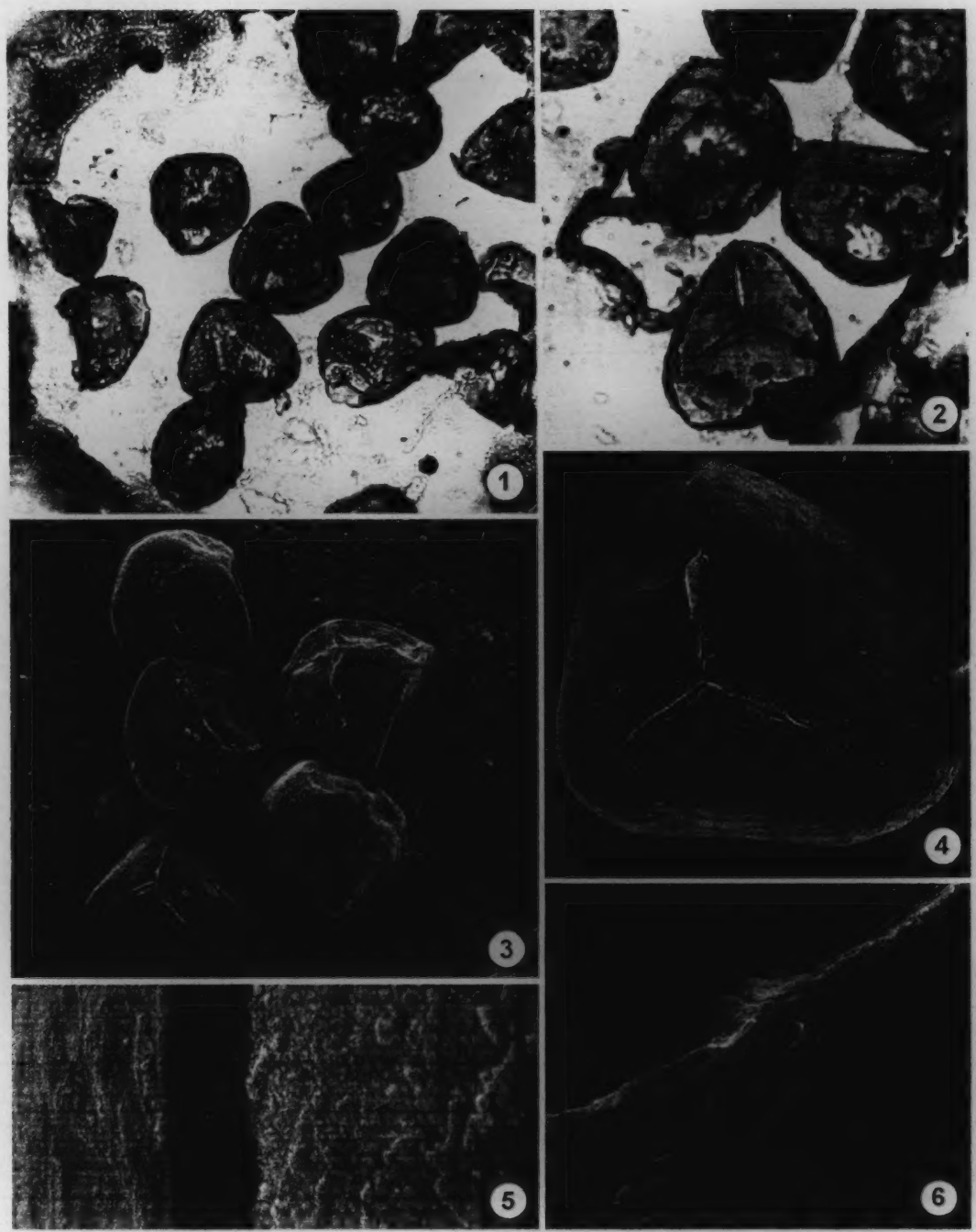
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Plate 11

Figs. 1-4. *Paralygodium meckertii*, three dimensional reconstruction.

Fig. 1. Three dimensional reconstruction of adaxial side of fertile pinnule (adaxial surface removed by saw cut). Laminar tissue is dark grey, pinnule midrib light grey, sporangia black. Paratype P14334 D. X 33.

Fig. 2. Three dimensional reconstruction of abaxial surface of pinnule. Note lateral major lobes dividing into three minor lobes and terminal major lobe is abraded. Paratype P14434 D. X 33.

Fig. 3. Three dimensional reconstruction of adaxial surface of pinnule. Note lateral major lobes dividing into three lobes each, and pinnule base. Paratype P14338 C top. X 41.

Fig. 4. Three dimensional reconstruction of abaxial side of pinnule (abaxial surface removed by saw cut). Note lateral lobes dividing into three minor lobes each and pinnule base. Paratype P14438 C top. X 41.

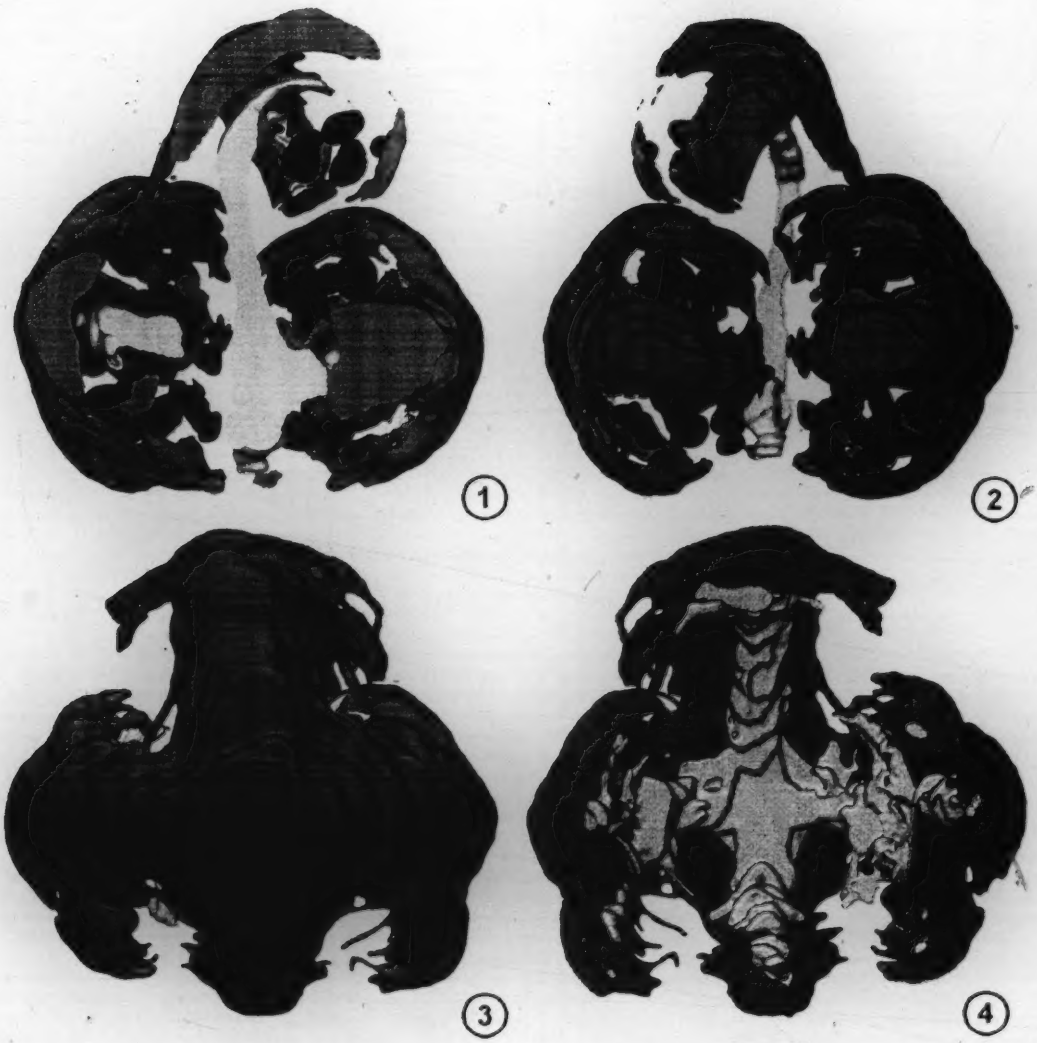
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Plate 12

Figs. 1-4. Cycadeoid with resin canals in the cortex and a woody eustele

Fig. 1. Cycadeoid stem. P14371 B. X 1.8.

Fig. 2. Enlargement of Fig. 1, showing cortex with resin canals (arrowheads). P14371 B. X 4.0.

Fig. 3. Transverse section of stem showing central pith, secondary vascular tissues, leaf trace (arrow) and cortex with mucilage ducts (arrowheads). P14371 Bot #72. X 3.0.

Fig. 4. Transverse section of stem showing insect gallery (center) lined by "nutritive tissue" (Nu), and cortex with mucilage ducts (arrowheads). P14371 top, #57. X 3.0.

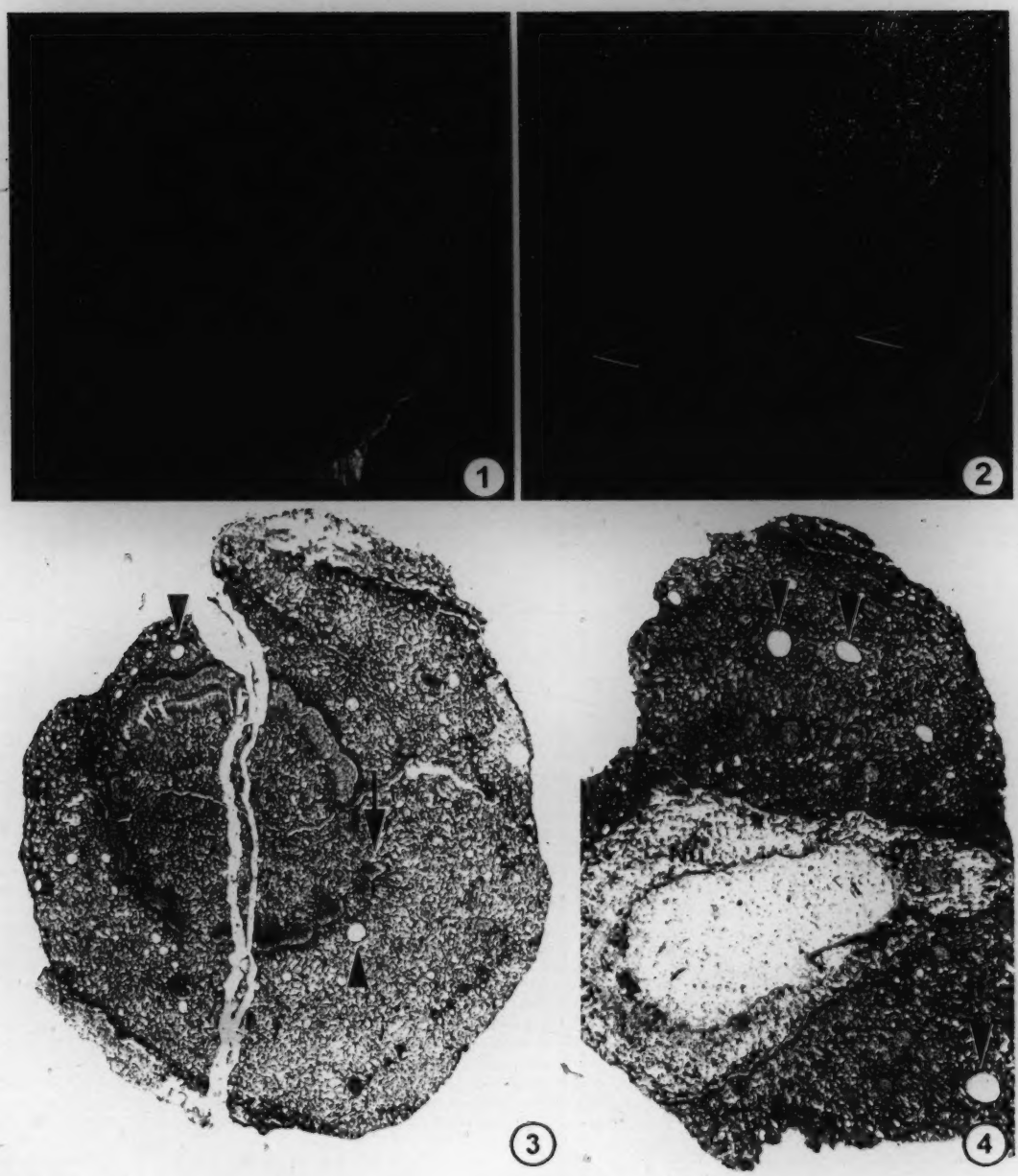
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Plate 13

Figs. 1-5. *Pinus* leaves in transverse section.

Fig. 1. Five-needle pine leaf. Note two vascular bundles, transfusion tissue (TT), endodermis (E), and abundant sclerenchyma. P14439 B bot #2. X 77.

Fig. 2. Five-ne Five-needle pine leaf. Note two vascular bundles, transfusion tissue, mesophyll (M), abundant sclerenchyma and three resin canals (R). P13347 E bot #1a. X 76.

Fig. 3. Five-needled pine epidermis from Fig. 1, showing epidermis (Ep) and cuticle (C). P14439 B bot #2. X 670.

Fig. 4. Three-needle pine leaf. Note two vascular strands, transfusion tissue (T), endodermis (E), and two resin canals (R). P14460 E top #1. X 76.

Fig. 5. Three-needled pine leaf showing plicate mesophyll (M) and resin canal (R). P14460 E top #1. X 181.

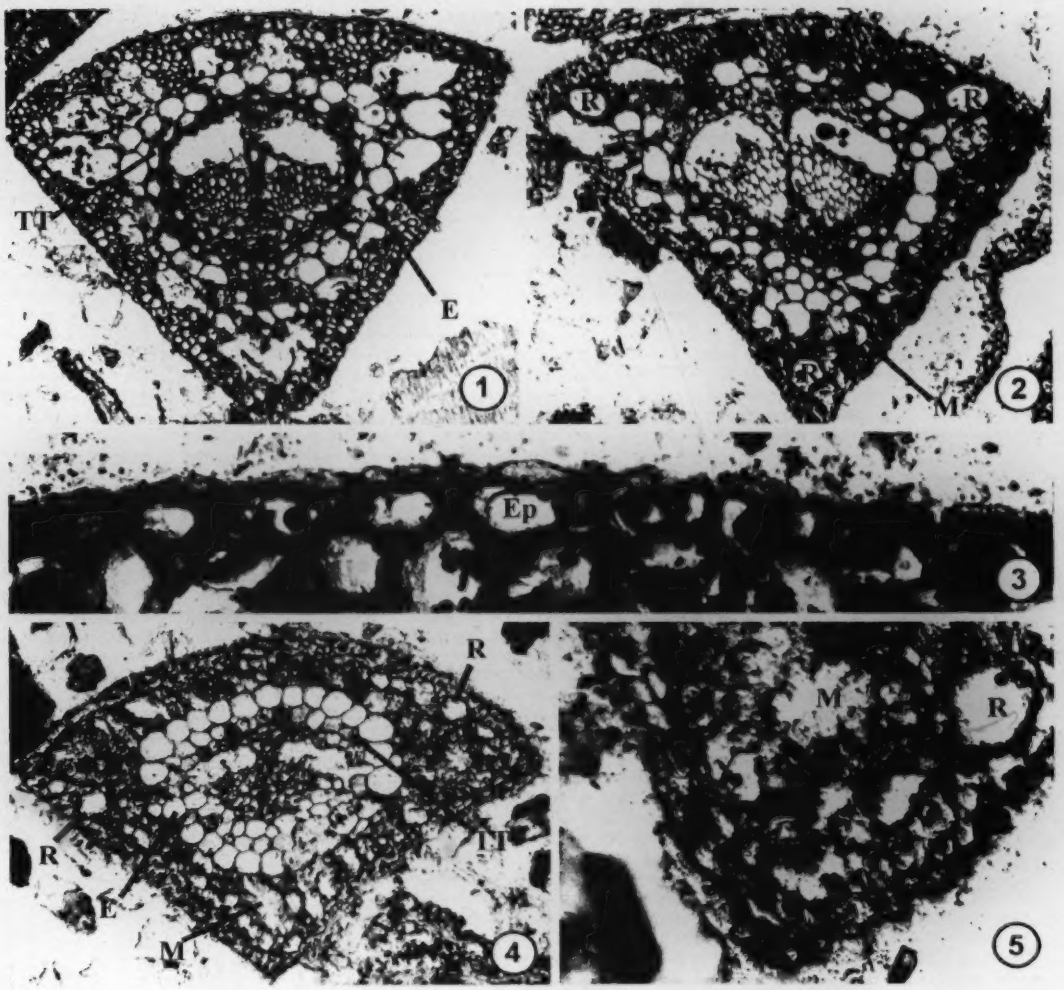
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Plate 14

Fig. 1-4. Pinaceous pollen cone and pollen.

Fig. 1. Pinaceous cone in longitudinal section (top) and transverse section (bottom). P14468 F bot #1. X 23.

Fig. 2. Pinaceous microsporophyll with abaxial two pollen sacs and vascular bundle (top). P14468 F bot #1. X 92.

Fig. 3. Pinaceous pollen sac with wall thickenings. P14468 F bot #1. X 91.

Fig. 4. Pinaceous bisaccate pollen. P14468 F bot #1. X 333.

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Plate 15

Figs.1-4. SEM images of bisaccate pollen grains from pinaceous cone P14468 F bot #6.

Fig. 1. Pollen grain. X 700.

Fig. 2. Broken pollen grain showing endoreticulations of the saccus. X 1000.

Fig. 3. Corpus with spinulose sculpturing. X 6000.

Fig. 4. Broken grain showing side view of saccus internal wall thickenings. X 5000.

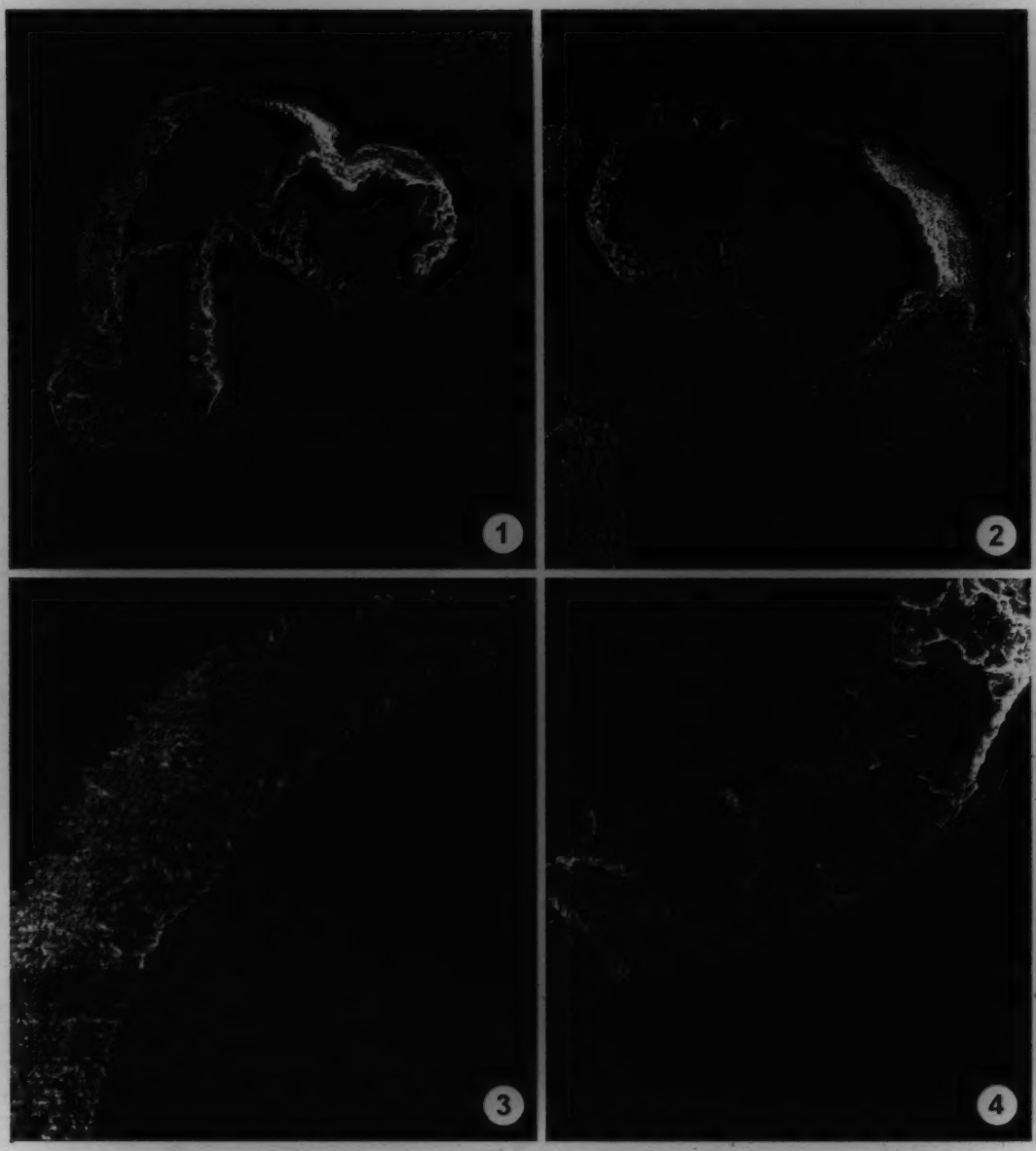
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Plate 16

Figs. 1-5. Organs of taxodiaceous Cupressaceae.

Fig. 1. Transverse section of twig with helically attached leaves. Note single large central resin canal. P14492 D #45. X 70.

Fig. 2. Longitudinal section of twig with attached leaves. P14334 D bot 1b. X 11.

Fig. 3. Transverse section of wood, showing pith, secondary xylem, lack of resin canals, and remains of periderm. P14345 E top 6d. X 50.

Fig. 4. Transverse section of twig with leaves and several pollen cones. Note microsporophyll with attached pollen sacs and subtending ensheathing leaves (SL). P15037 B bot #2. X 14.

Fig. 5. Sporophyll with adaxial vascular bundle (top) and four attached pollen sacs (arrows). P15037 B bot #2. X 45.

Fig. 6. Pollen sac with pollen. P15037 B bot #2. X 100.

Fig. 7. Transverse section of leaf c.f. *Cunninghamia*. Note central resin canal. P14320 B bot #1a . X 43.

Fig. 8. Transverse section of leaf c.f. *Cunninghamia* showing stele and winged transfusion tissue. Note one resin canal (R), tracheids (T). P14320 B bot # 1a. X 214.

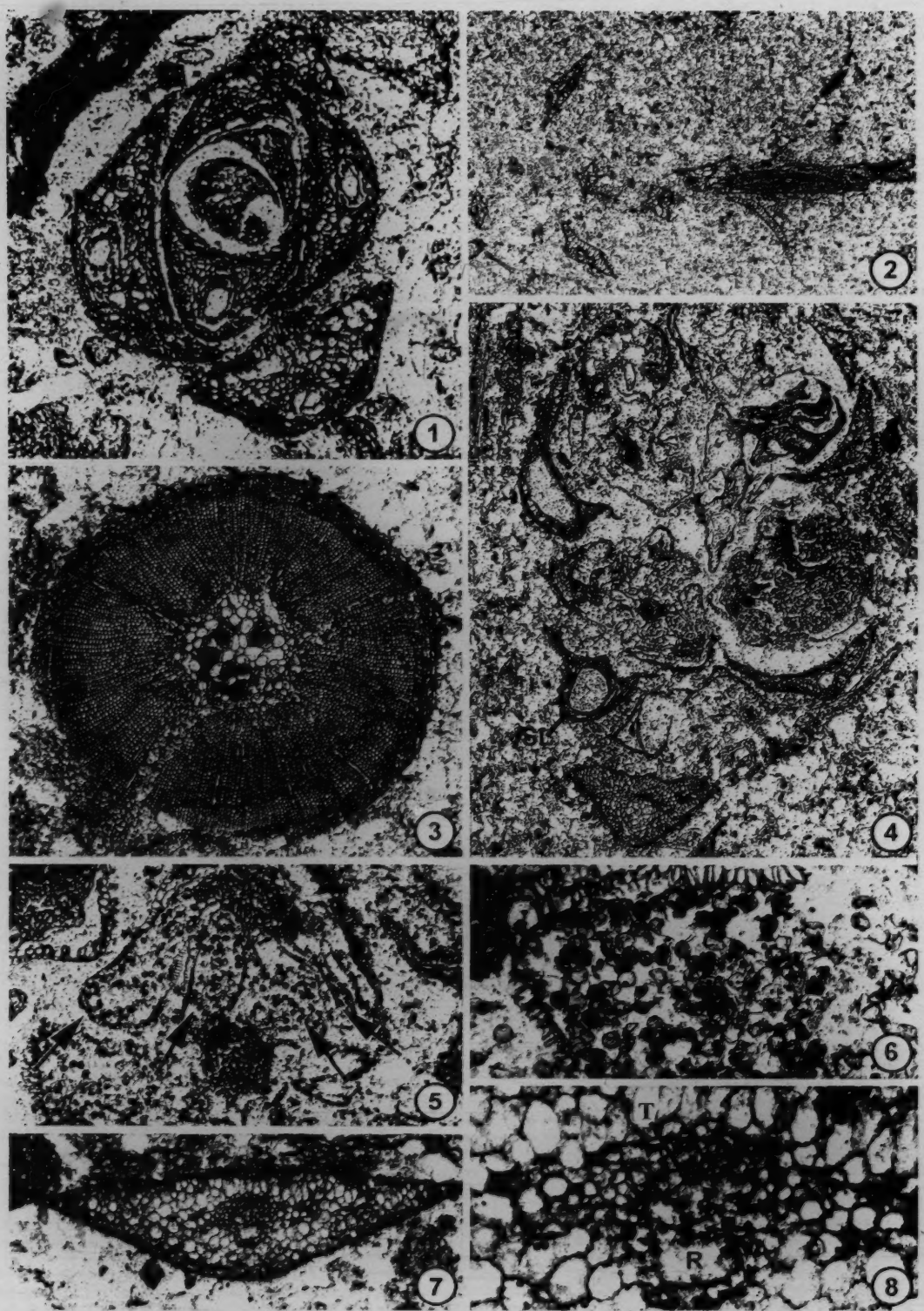
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Plate 17

Figs. 1-5. Conifer seed, *cf. Araucaria*

Fig. 1. Longitudinal section of conifer seed with wavy nucellar apex. P14465 C bot #5. X 7.5.

Fig. 2. Integument showing sclerotesta (Sc), and endotesta (En). P14465 D top #7. X 90.

Fig. 3. Conifer seed showing wavy nucellar apex. Note endotesta (En) and possible megagametophyte (M). P14465 C bot #5. X 40.

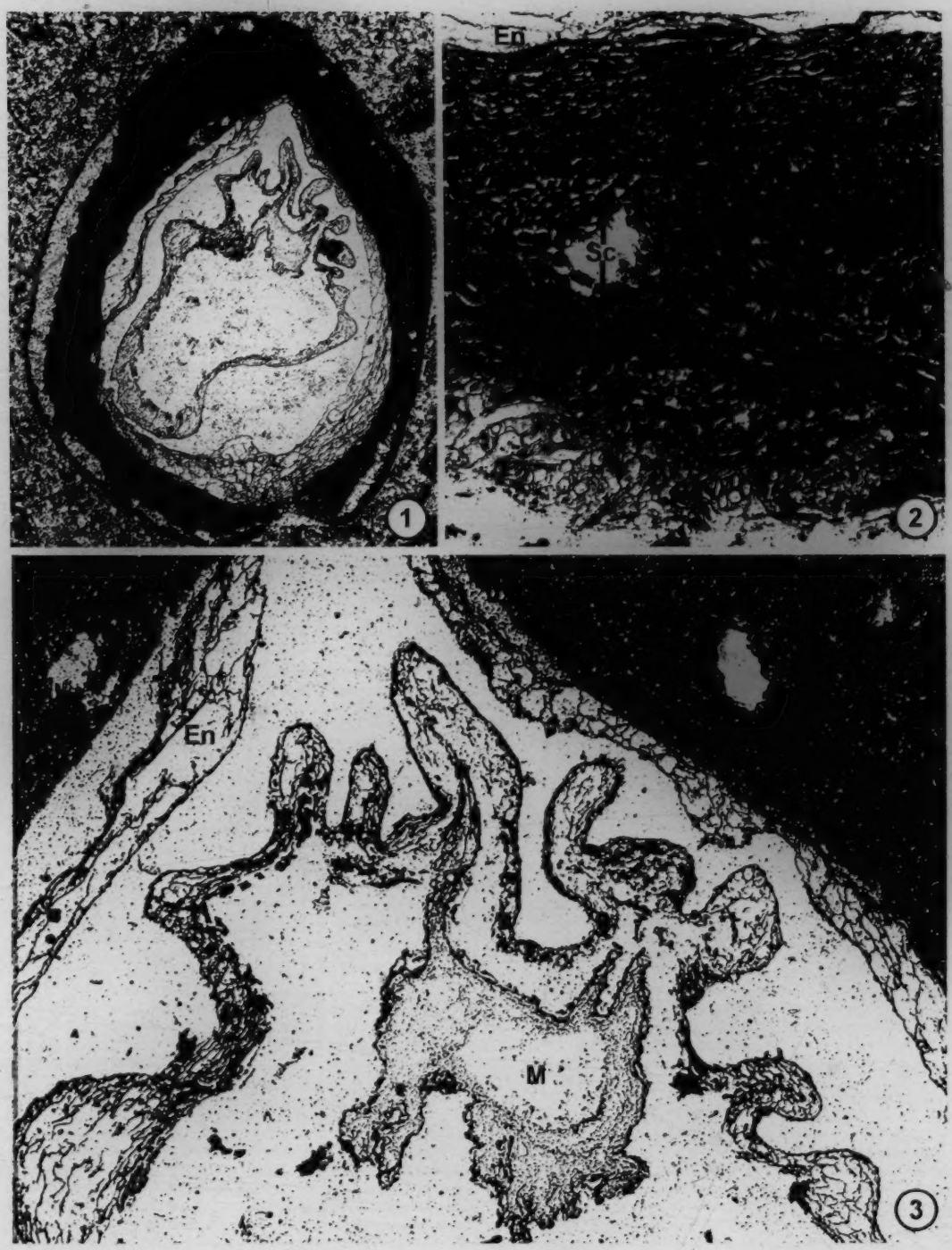
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Plate 18

Figs. 1-4. Lauraceous flower and inflorescences.

Fig. 1. Longitudinal section of isolated flower. Note single carpel, anthers, tepals, and receptacle. P14347 D bot #4a. X 37.

Fig. 2. Oblique longitudinal section of isolated inflorescence showing flowers with subtending bracts (B). All structures contain idioblasts (I) and trichomes. (T). P13527 I #1a. X 26.

Fig. 3. Oblique transverse section of flower in lauraceous inflorescence, showing central gynoecium (G), numerous stamens (S) and at least two whorls of perianth. P12527 I #1a. X 96.

Fig. 4. Cross section of inflorescence showing central axis, developing flowers, subtending bracts, numerous idioblasts, and trichomes. P14400 C bot #1. X 48.

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Plate 19

Figs. 1-3. Lauraceous fruit.

Fig. 1. Longitudinal section of immature fruit with two layers of overarching tepals. Note fleshy mesocarp (M), palisade endocarp (E), seed integument (I), and idioblasts throughout. P14465 B bot #1. X 36.

Fig. 2. Tracheary elements with spiral or scalariform secondary wall thickenings. P14465 B bot #1. X 416.

Fig. 3. Palisade endocarp. Note fungal hypha (arrowhead). P14465 B bot #1 x 145.

Fig. 4. Staminal remains. Note stamen (S), integument (I), idioblasts in mesocarp (arrows) P14465 B bot #1. X 152.

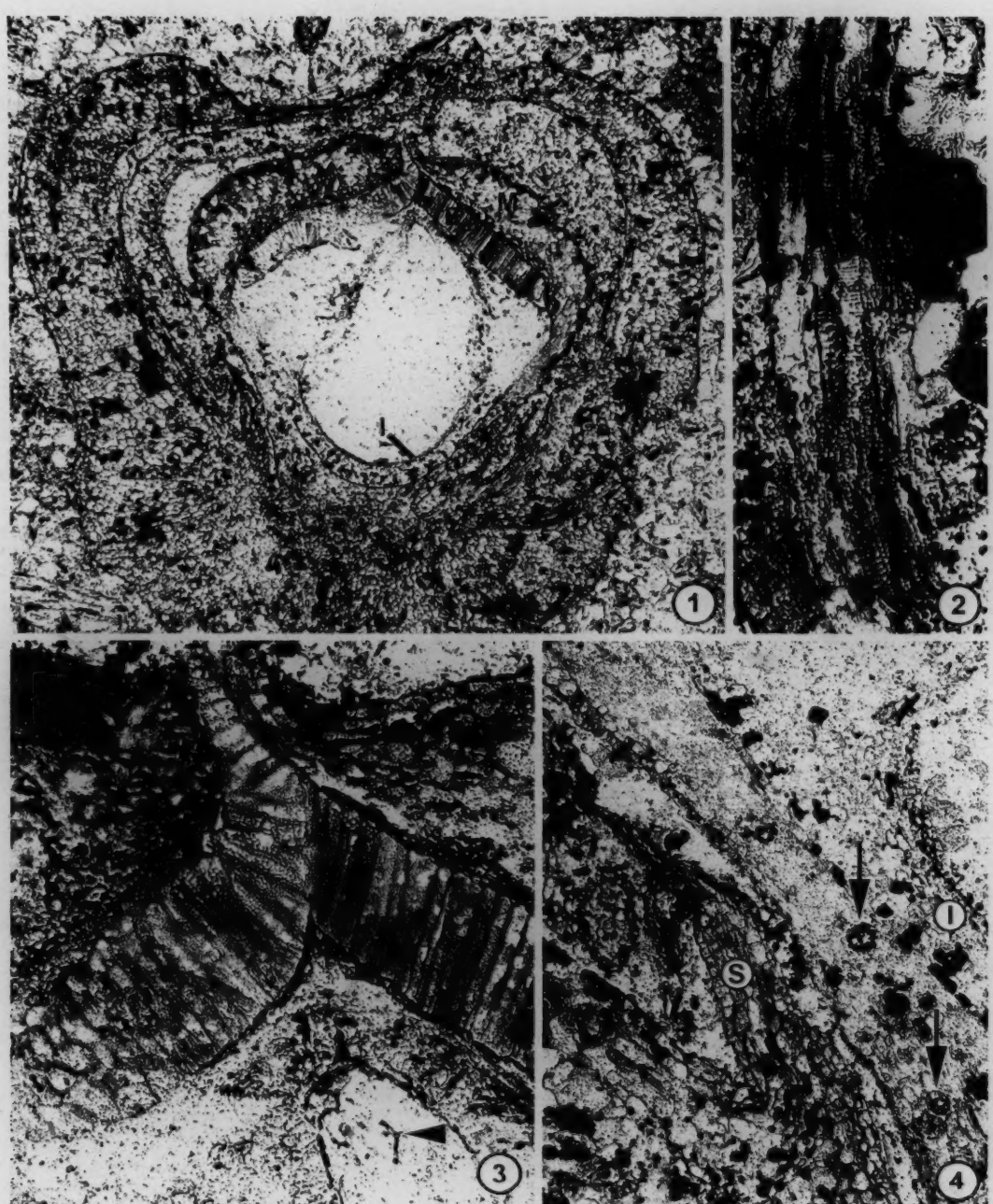
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Plate 20

Figs. 1-5. Transverse sections of angiosperm wood *cf. Paraphyllanthoxylon*.

Fig 1. Oblique transverse section of wood showing vessels. P15041 C top #1 x 5.

Fig 2. Pith parenchyma. P15041 C top #1. X 51.

Fig. 3. Secondary xylem showing vessels in radial multiples. P15041 C top #1 x 83.

Fig 4. Vessels in radial multiples. P15041 C top #1. X 48.

Fig 5. Transverse section of dicot wood showing uniseriate and multiseriate rays and vessels with tyloses (arrows). P14457 E top #1c. X 75.

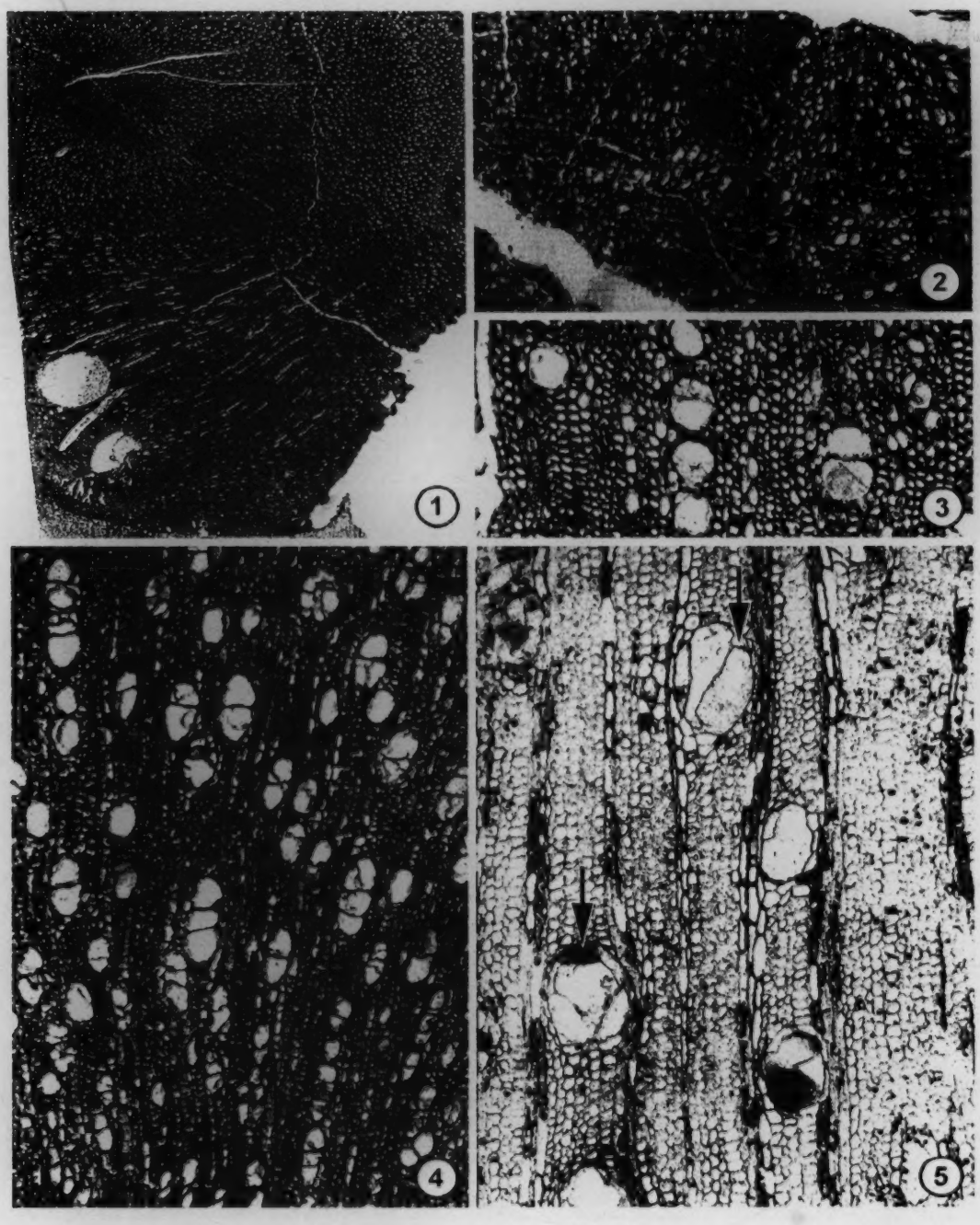
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Plate 21

Figs. 1-4. Radial longitudinal section of angiosperm wood *cf. Paraphyllanthoxylon*.

P15041 C side b2 #4.

Fig. 1. Vascular rays. X 56.

Fig 2. Rays and four vessel members of radial multiple. X 125.

Fig. 3. Wood fibers and vessel element with tyloses (arrow). X 92.

Fig. 4. Round to elongate. ray-to-vessel pitting. X 250.

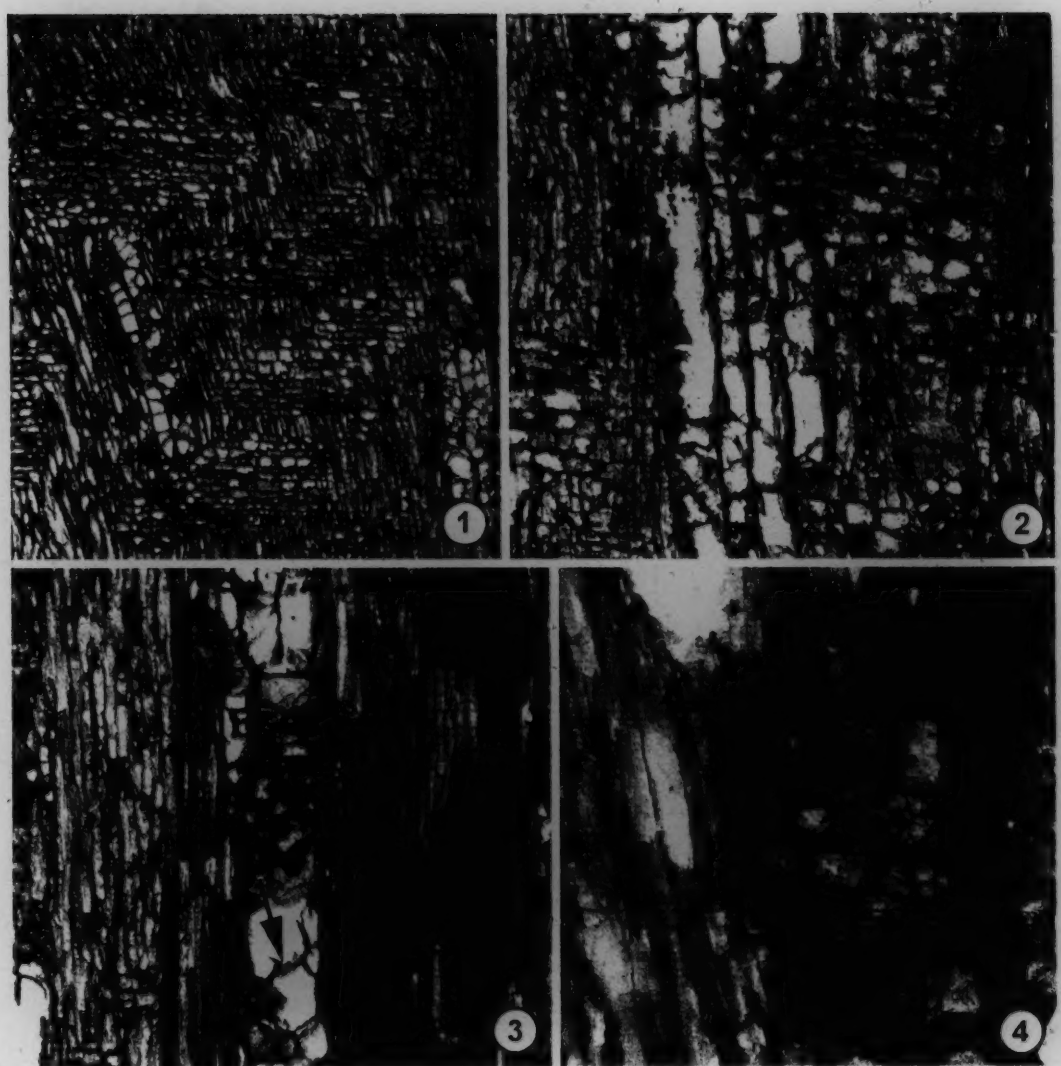
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Plate 22

Figs. 1-4. Tangential longitudinal section of angiosperm wood *cf. Paraphyllanthoxylon* P15041 C side c #1.

Fig. 1. Vessel elements and rays. X 42.

Fig. 2. Vessel elements showing simple perforation plates (arrows), and rays in section. X 111.

Fig. 3. Vessel showing alternate intervessel pitting. X 315.

Fig. 4. Bi and tri-seriate rays and septate wood fibers (arrows). X 194.

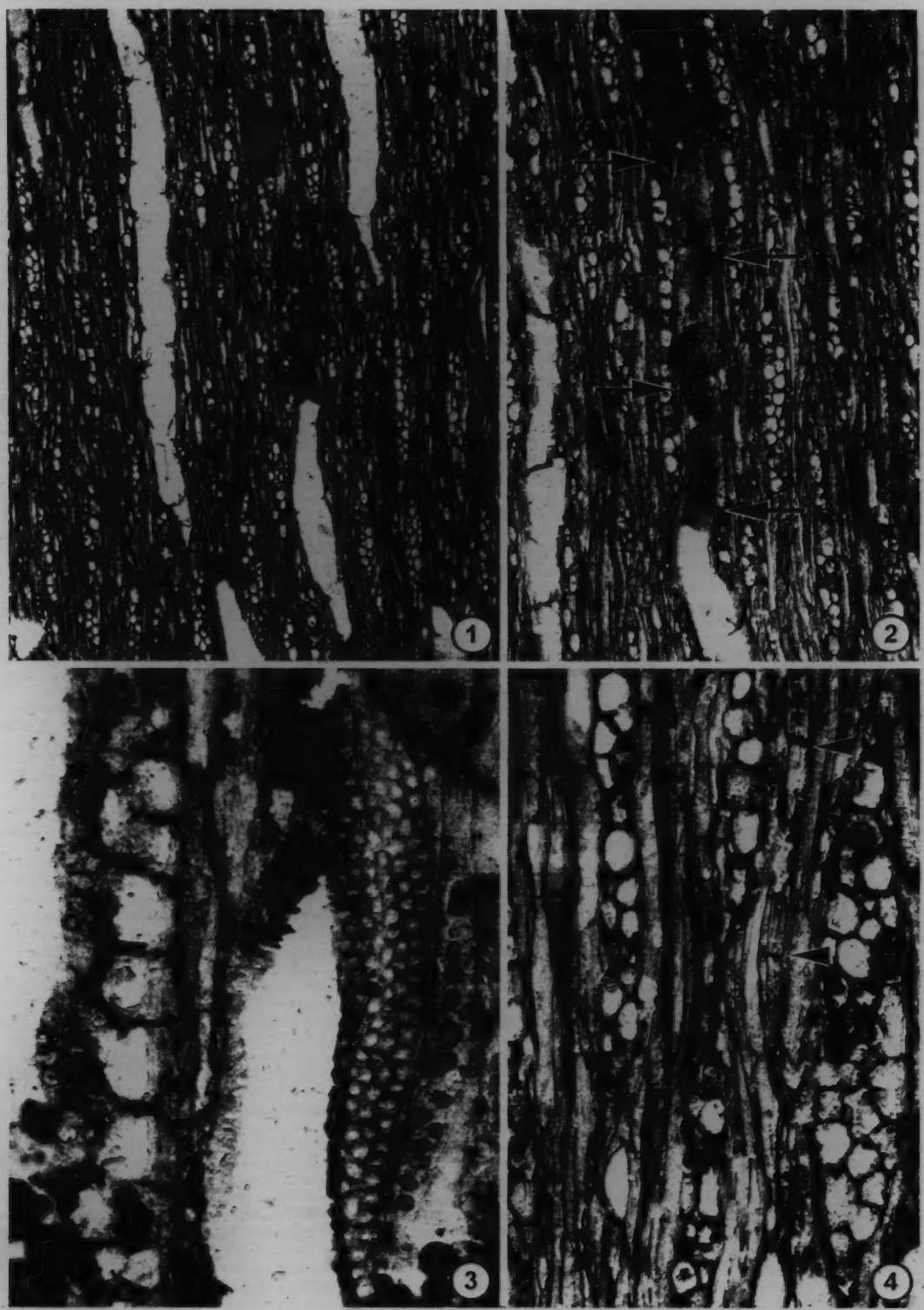
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Plate 23

Figs. 1-6. Inflorescences and fruits.

Fig. 1. Longitudinal section of receptacle of platanaceous inflorescence, showing numerous flowers. P14460 E bot #6. X 16.

Fig. 2. Longitudinal section of platanaceous inflorescence showing parenchymatous receptacle, and flower with five carpels, stamens with pollen, and tepals. P14460 F top #32. X 22.

Fig. 3. Enlargement of flower in Fig. 2, showing five carpels and stamen (S). P14460 F top #32. X 40.

Fig. 4. Fruits with winged seeds and remains of tepals (arrows). P14468 C botb # 74. X 44.

Fig. 5. Longitudinal section of platanaceous anther with prolate tricolpate pollen grains. P14460 E bot # 11. X 513.

Fig. 6. Cross section of ?saxifragalean infructescence showing parenchymatous receptacle, and abraded two-loculed fruits. P14470 D bot #1. X 22.

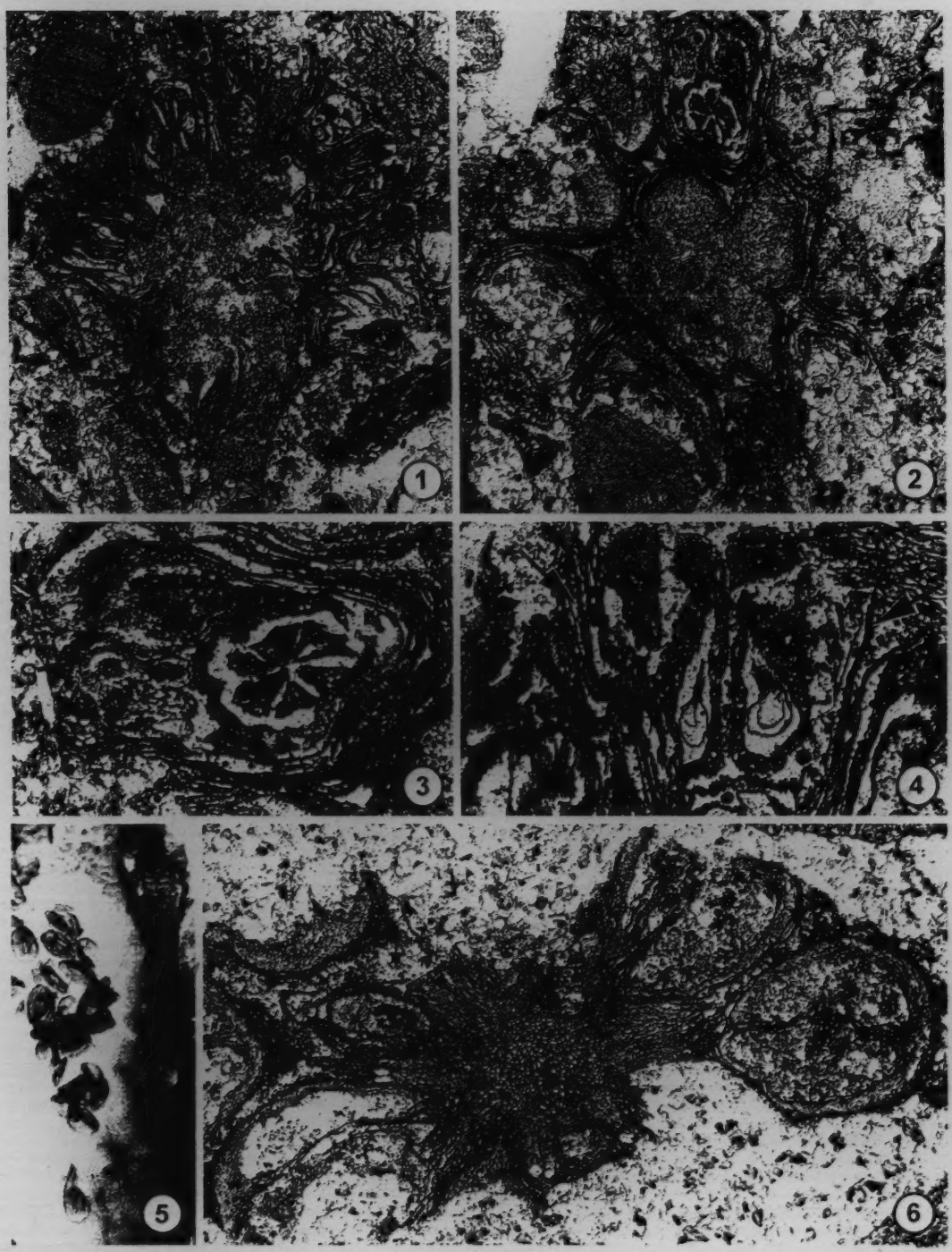
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Plate 24

Figs. 1-4. SEM of platanaceous pollen P14460 E bot #7.

Fig. 1. Pollen with microreticulate tectum. X 2100.

Fig. 2. Tricolpate pollen showing granular aperture sculpture (top). X 6700 .

Fig. 3. Platanaceous tricolpate pollen grain with reticulate exine. X 6000.

Fig. 4. Broken platanaceous pollen grain showing tectate collumellate exine. Note smaller ?fungal spore. X 8000.

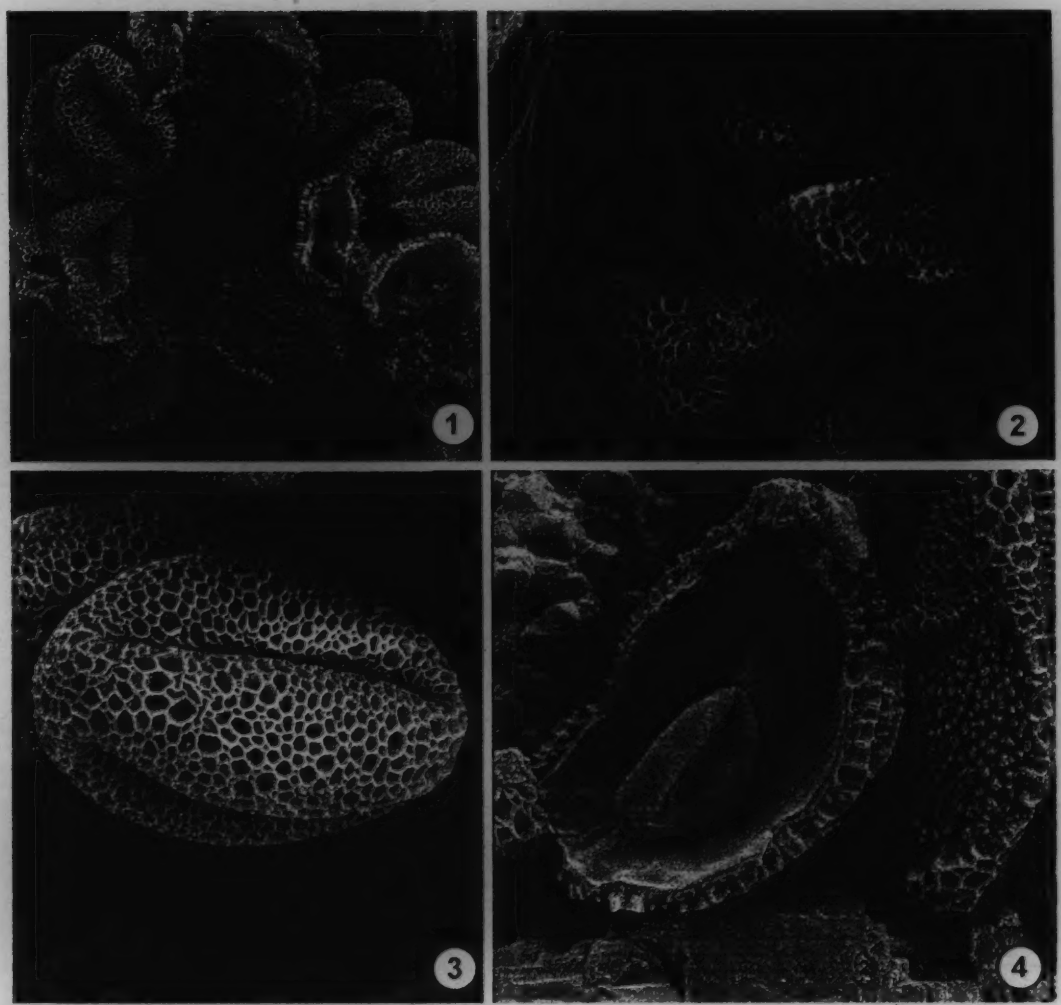
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Plate 25

Figs. 1-5. Nyssaceae fruits in transverse section.

Fig. 1. Ridged fruit with three locules and germination valves. P13037 C bot #1a. X 20.

Fig. 2. Four-loculed fruit with contents showing germination valves. P13527 C bot #1a. X 23.

Fig. 3. Enlargement of specimen in Fig. 4. Note small rectangular cells lining locule (arrows), and elongate fibers of endocarp. Note suture of germination valve (V). P13527 C bot # 2a. X 100.

Fig. 4. Three-loculed fruit with fleshy pericarp. P14604 B top #2. X 22.

Fig. 5. Pericarp with fibrous bundle (B) and endocarp with elongate fibers (F). P14604 B top #2. X 62.

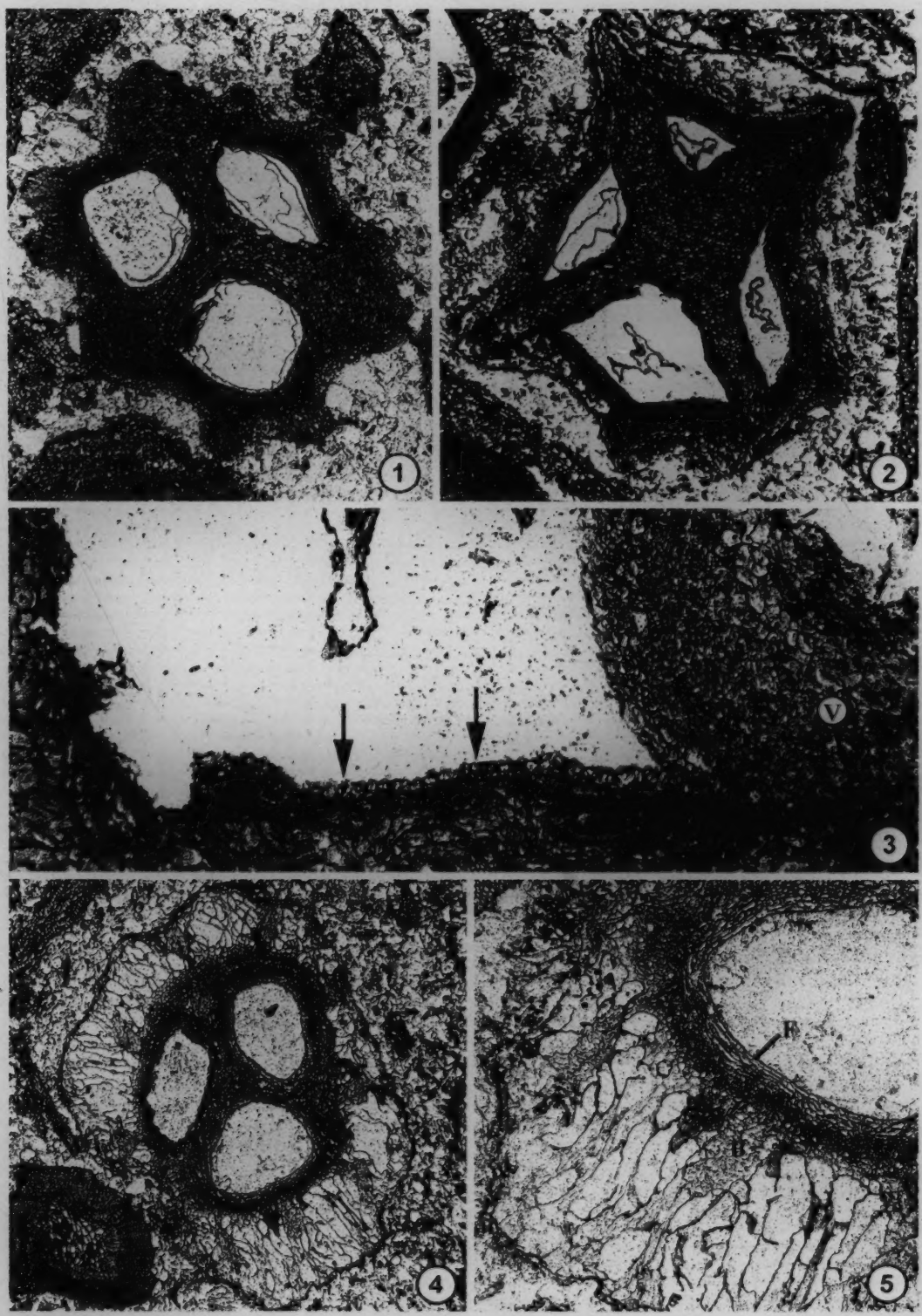
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Plate 26

Figs. 1-2. Longitudinal section of ?cornalean fruit.

Fig. 1. Longitudinal section of drupaceous fruit showing two locules. Note short palisade cells lining locules, and sclerotic endocarp. P14467 A #1a. X 36.

Fig. 2. Enlargement of fruit at septum, showing sclerotic endocarp with palisade cells lining locules. P14467 A #1a. X 107.

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Plate 27

Figs. 1-6. ?Ericalean fruits.

Fig. 1. Three loculed fruit with seeds, sclerotic endocarp with fleshy tepals (near bottom). Note possible lines of dehiscence (arrowheads). P14492 C bot #85b. X 34.

Fig. 2. Mesophyll (M) and epidermis (E) in specimen seen in Fig. 1, showing parenchymatous cells, some with dark contents. P14492 C bot #36b. X 158.

Fig. 3. Enlargement of spiny seeds seen in Fig. 1. P14492 C bot #85b. X 130.

Fig. 4. Oblique longitudinal section of multi-loculed ?ericalean fruit. P14489 B top #1a. X 23.

Fig. 5. Seeds attached to placenta (at left). P14489 B top #1a. X 75.

Fig. 6. Transverse section of peduncle showing parenchymatous cortex and secondary xylem. P14489 B side 2 #1. X 40.

Fig. 7. Longitudinal section of fruit in Fig. 4, at more distal level showing pedicel (Pe), crushed, perianth (P) and fleshy cupule (arrow). P14489 B top #30. X 12.

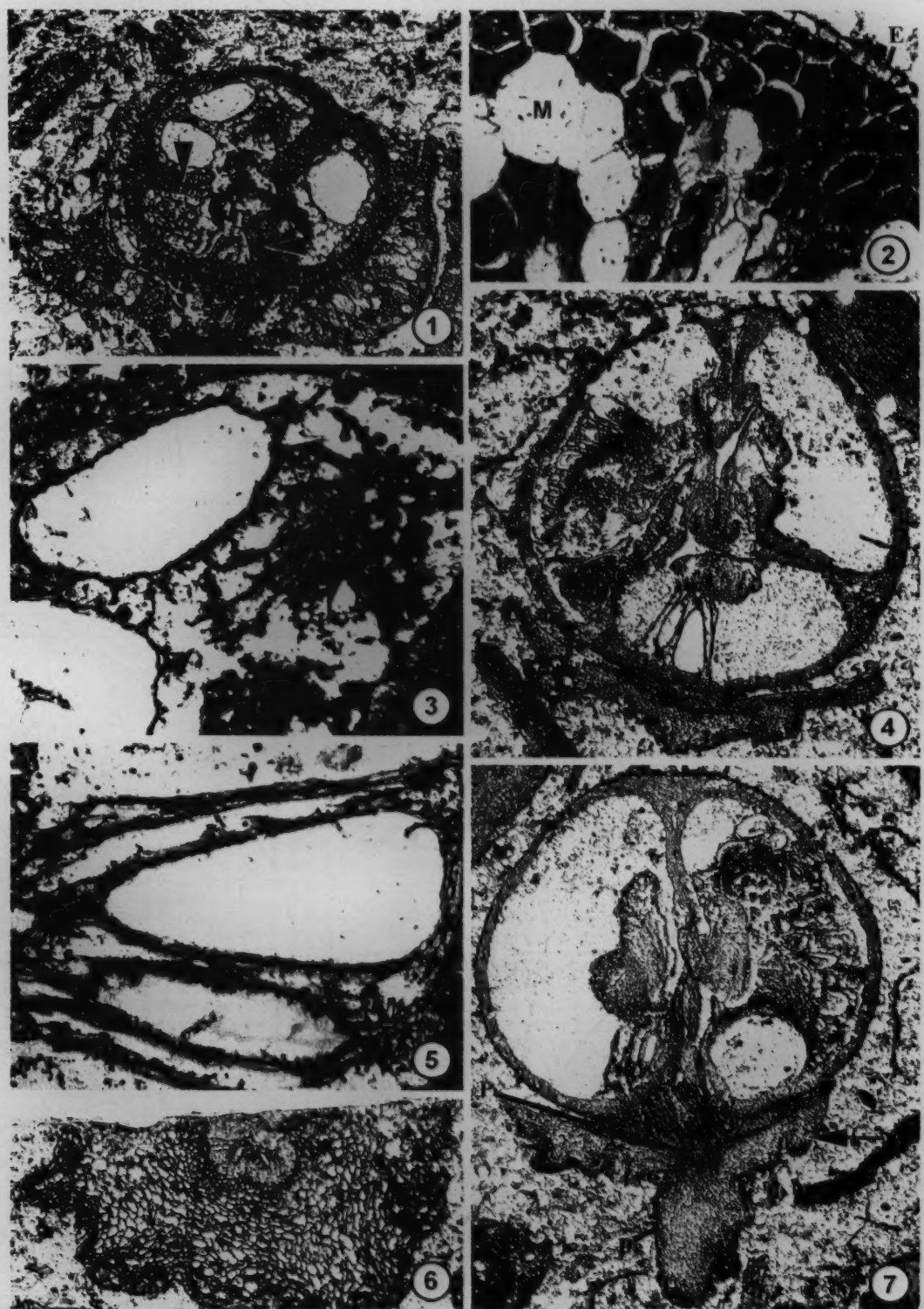
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Plate 28

Figs. 1-2. ?Ericalean fruit.

Fig. 1. Longitudinal section of fruit with remains of perianth (arrow), and spiny/ridged seeds. P14468 E top # 19. X 46.

Fig. 2. Enlargement of spiny/ridged seeds in Fig. 2. P14468 E top #19. X 125.

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Plate 29

Figs. 1-5. One, two and three-loculed fruits of unknown affinities.

Fig. 1. Transverse section of unknown fruit 1, with two sutures and ridged endocarp. P15037 A #3b. X 23.

Fig. 2. Enlargement of Fig. 2, showing two zones of stony endocarp at suture. P15037 A #3b. X 119.

Fig. 3. Transverse section of unknown fruit 2, with two locules and possible central vascular bundle (arrow). P14347 E bot # 4c. X 42.

Fig. 4. Enlargement of one locule from Fig. 3, showing short palisade cells lining locule, parenchymatous pericarp and interlocking cells of integument. P14347 # 4c E bot. X 330.

Fig. 5. Transverse section of unknown fruit 3, showing, three-locules and central vascular strand. P14462 F top #1. X 56.

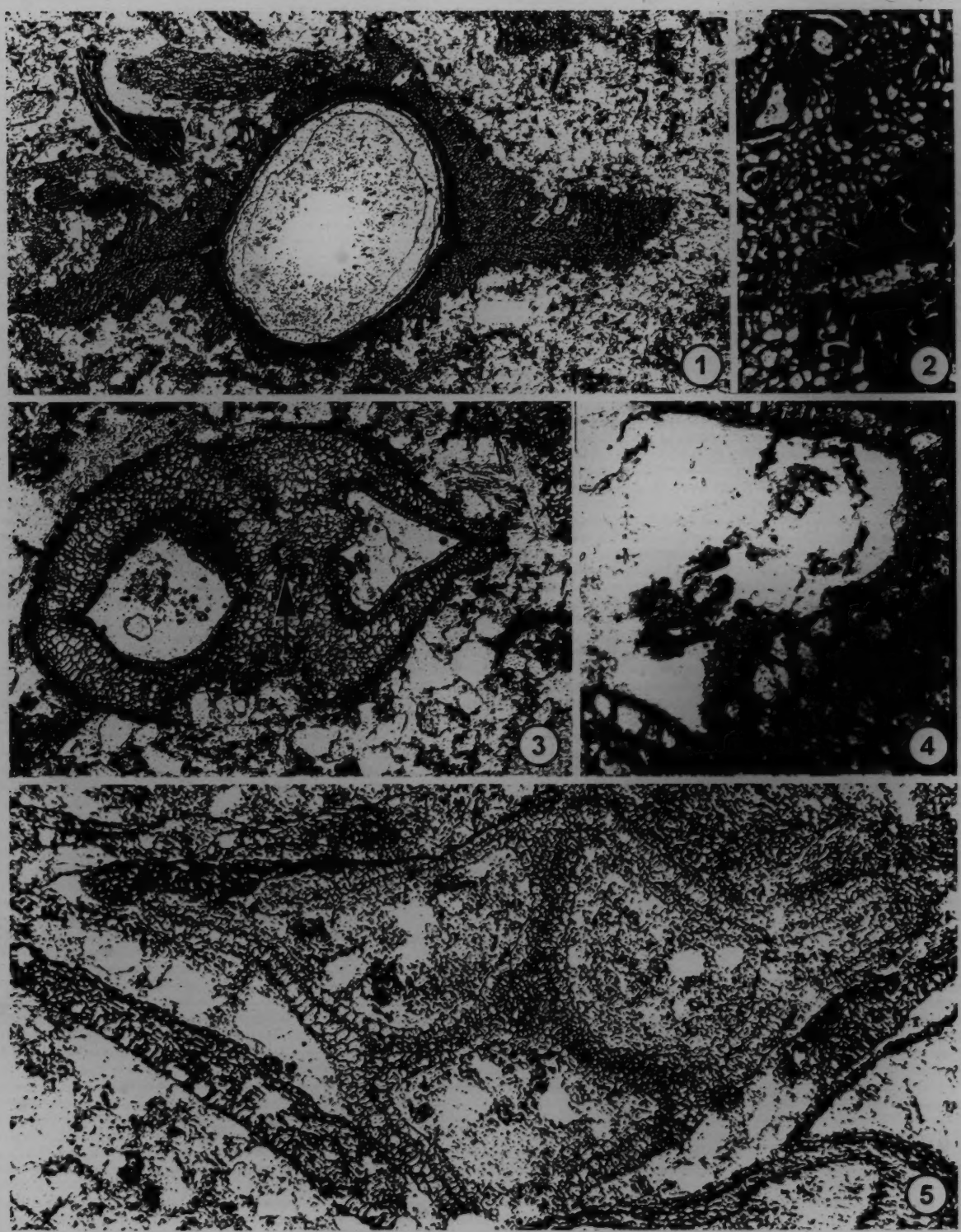
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Plate 30

Figs. 1-6. Three-loculed fruits of unknown affinities.

Fig. 1. Transverse section of unknown fruit 4, showing three locules and central vascular strand P14320 B bot #16d. X 48.

Fig. 2. Enlargement of locule seen in Fig.1, showing sclerotic endocarp and palisade cells lining locule. P14320 B bot #16d. X 309.

Fig. 3. Fusainized fruit (unknown fruit 5), with three locules with contents. Note fruit surrounded by three ?sepals. P14492 C bot #169c. X 32.

Fig. 4. Enlargement of locule from Fig. 3, showing seed. P14492 C bot #169c. X 79.

Fig. 5. Unknown fruit 6, with sclerotic endocarp and fleshy mesocarp. P14467 B top #1b. X 26.

Fig. 6. Enlargement of fruit in Fig. 5, showing sclerotic endocarp (top) with suture (arrow), and parenchymatous mesocarp (M). Note possible exocarp at bottom. P14467 B top #1b. X 93.

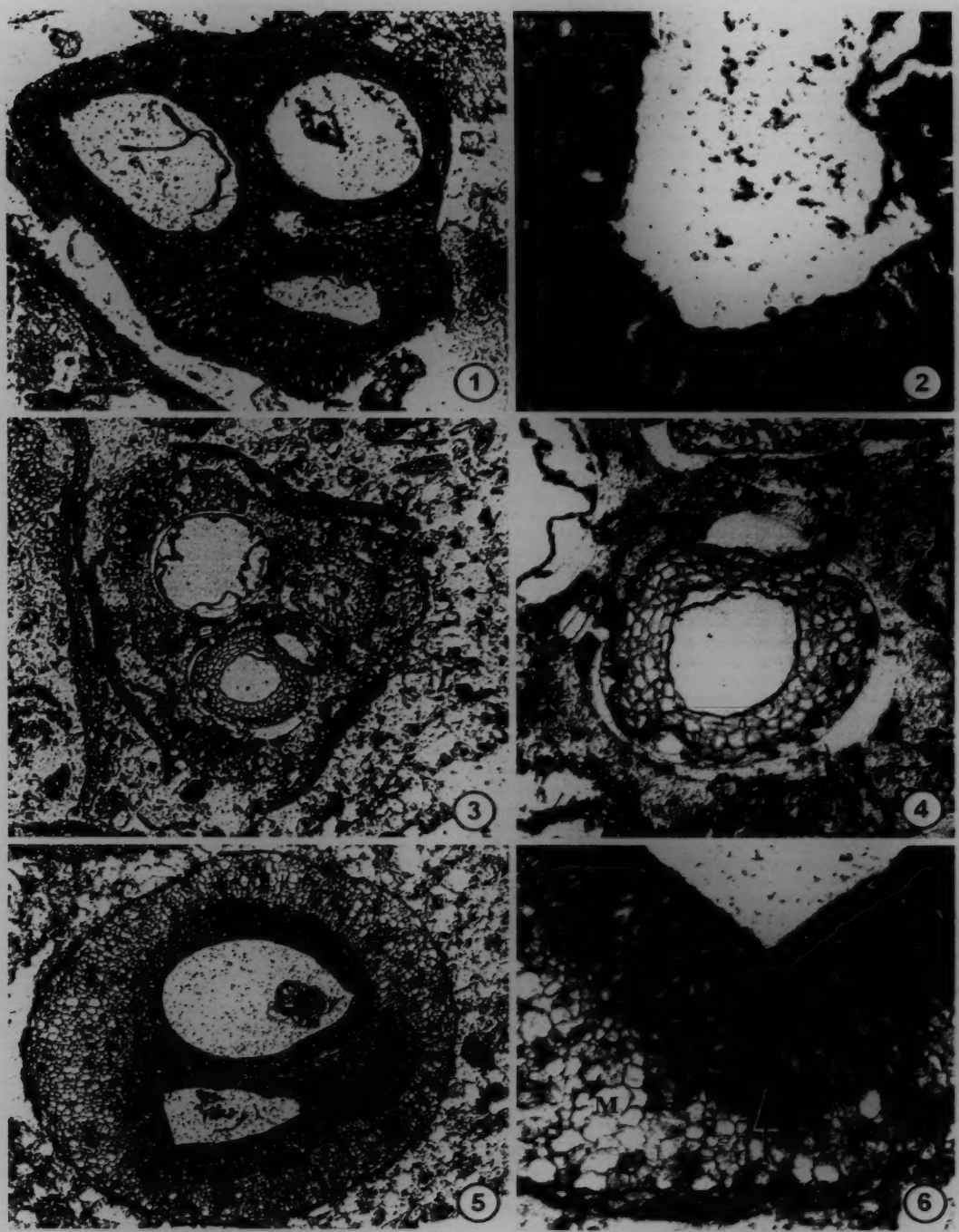
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Plate 31

Figs. 1-5 Multi-loculed fruits of unknown affinities.

Fig. 1. Transverse section of unknown fruit 7, showing five-locules and ridges. P14460 G top #1. X 14.

Fig. 2. Transverse section of unknown flower showing five-locules, remains of perianth, and three stamens with introrse dehiscence. P14320 E bot #4b. X 52.

Fig. 3. Transverse section of unknown fruit 8, with six-locules and fleshy mesocarp. P14319 B top #1a. X 25.

Fig. 4. Enlargement of locule from Fig. 3, showing seed, sclerotic endocarp, and fleshy mesocarp. Note narrow cells extending from locule representing possible zone of dehiscence (arrow). P14319 B top #1a. X 56.

Fig. 5. Enlargement of mesocarp cells showing pitting. P14319 B top #1a. X 571.

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Plate 32

Figs. 1-4. Septate ovoid fruit (unknown Fruit 9).

Fig. 1. Ovoid fruit with partitions (arrows) and enclosed seeds. P14546 G #1. X 12.

Fig. 2. Transverse section of similar fruit seen in Fig. 1, showing partitions and numerous fibrous bundles (arrows). P14489 C bot #2. X 23.

Fig. 3. Longitudinal section of partition showing tracheary elements with scalariform thickenings. P14546 G #1. X 375.

Fig. 4 Enlargement of specimen in Fig. 1, showing partition (bottom) and seed (S). P14546 G #1. X 59.

Fig. 5. Enlargement of specimen in Fig. 2. showing seeds, seed coat (SC) and fiber bundle (B). P14489 C bot #2. X 70.

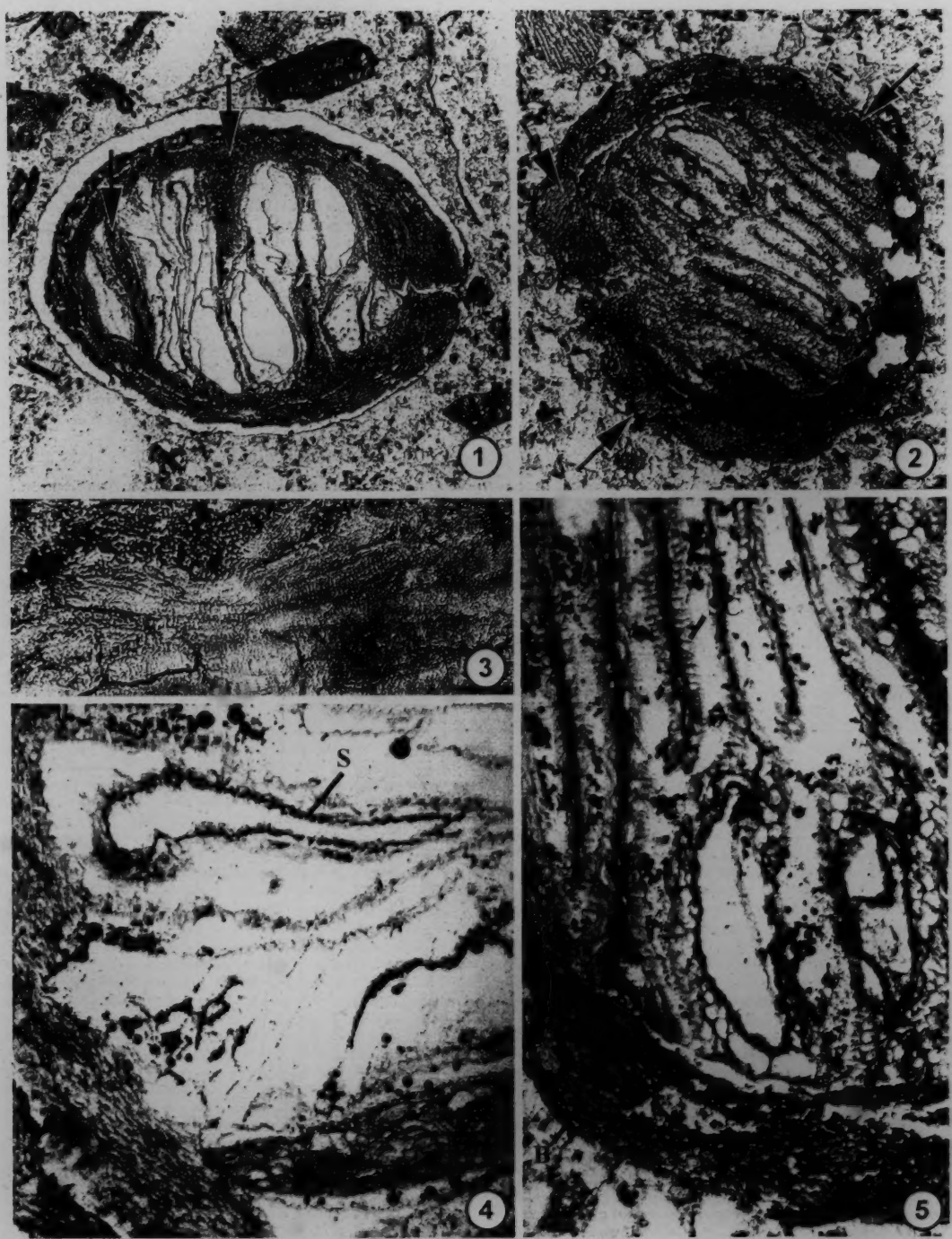

1
2
3
S
4
C
B
5

Plate 33

Figs. 1-3. Ridged fruits/seeds (unknown Fruit 10).

Fig. 1. Sclerotic ridged fruit. P14468 F bot #2a. X 23.

Fig. 2. Enlargement of Fig. 1, showing sclerotic endocarp and remains of mesocarp between ridges. P14468 F bot #2a. X 36.

Fig 3. Ridged fruit/seed on external surface of nodule showing central vascular. P14332 A. X 9.5 .

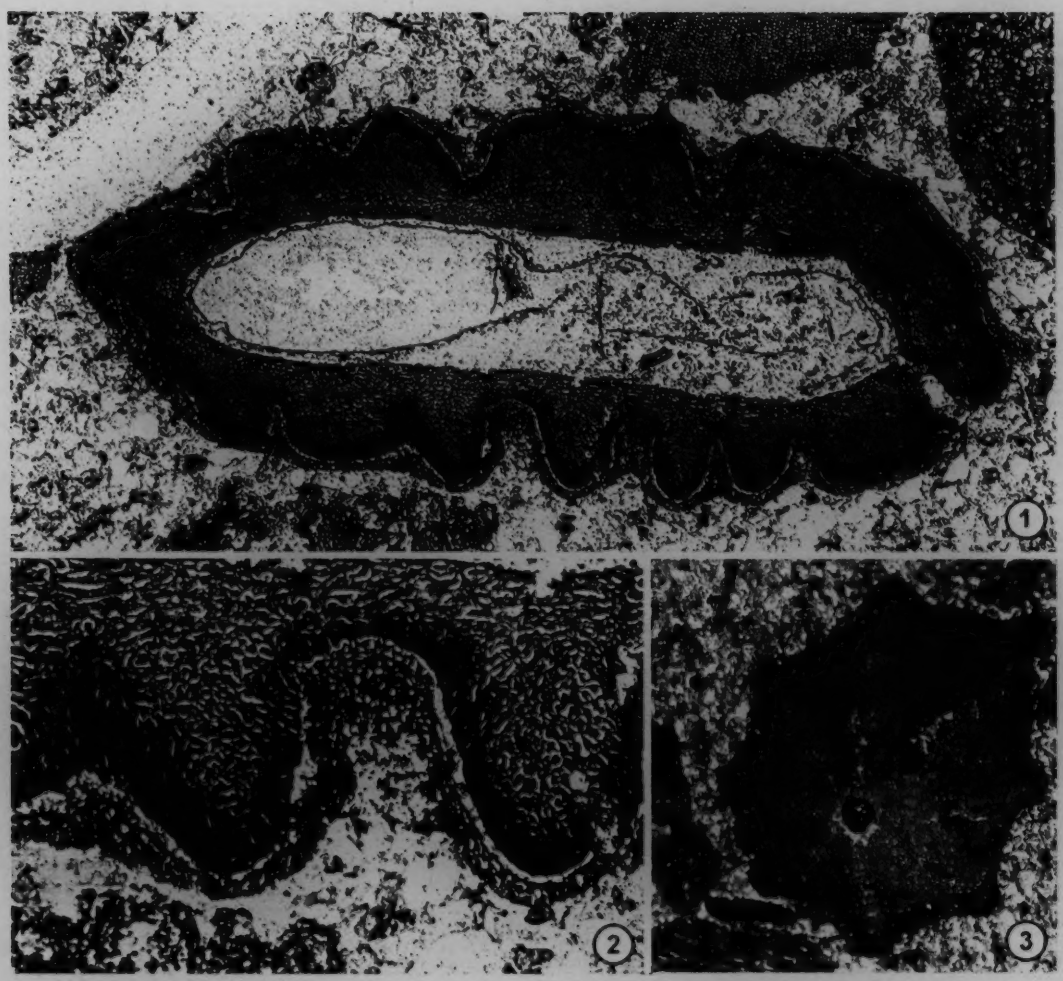

1
2
3

Plate 34

Figs. 1-4. Winged fruits of unknown affinity.

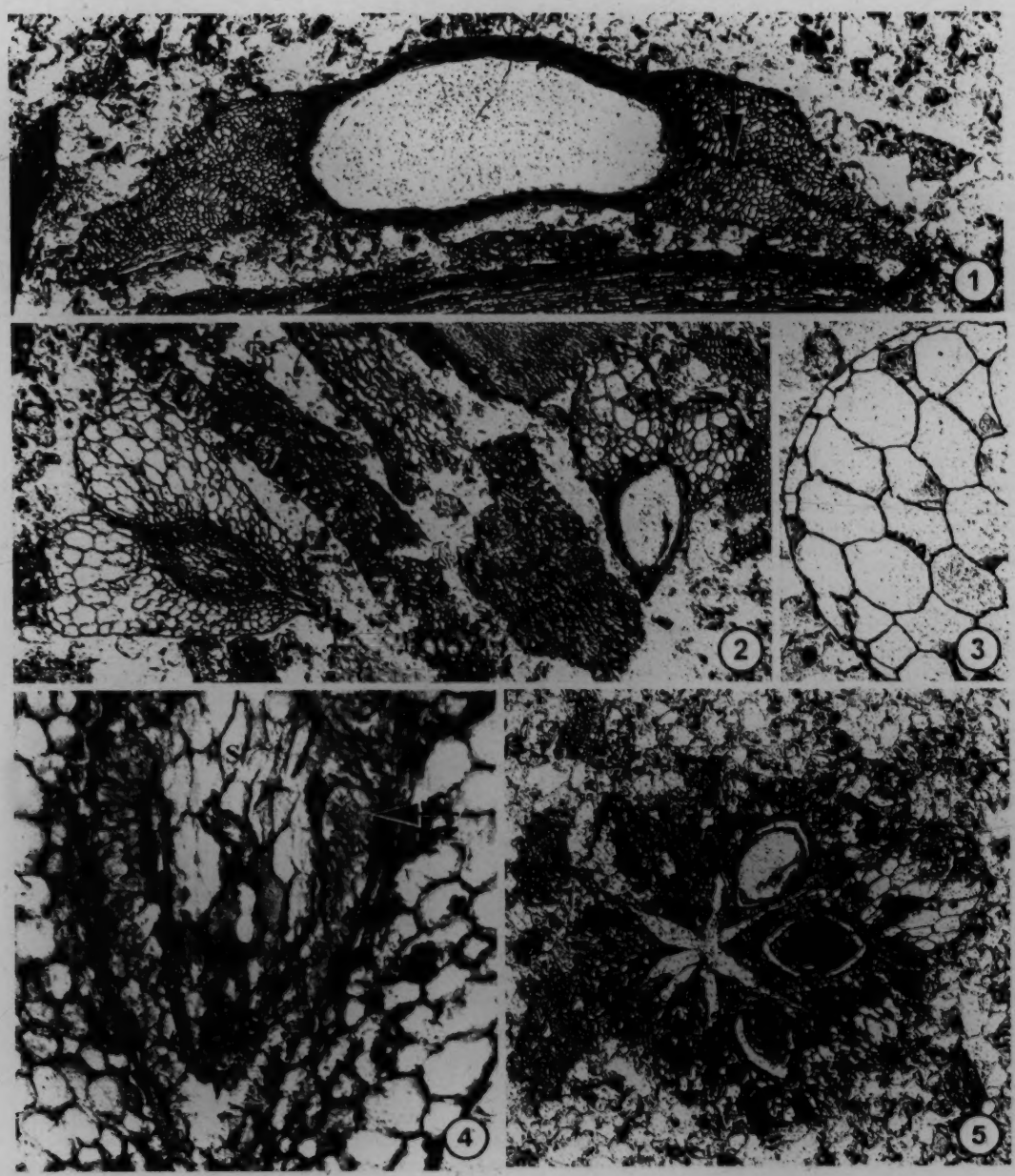
Fig. 1. Unknown fruit 11, with two wings. Note ?suture in wing (arrow) P13527 H #1c. X 34.

Fig. 2. Longitudinal section of two heart-shaped mericarps (unknown fruit 12). P14355 C top #3. X 30.

Fig. 3 Wing showing exocarp and mesocarp. P14605 B top # P14465 B top #22. X 62.

Fig. 4. Heart-shaped mericarp showing small thick-walled cells of endocarp (arrow) and larger thin-walled cells of wing, and seed body (S). P14355 C top #3. X 137.

Fig. 5. Schizocarp divided into six heart-shaped mericarps, some with contents. P14605 B top #1. X 161.


1
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3
4
5

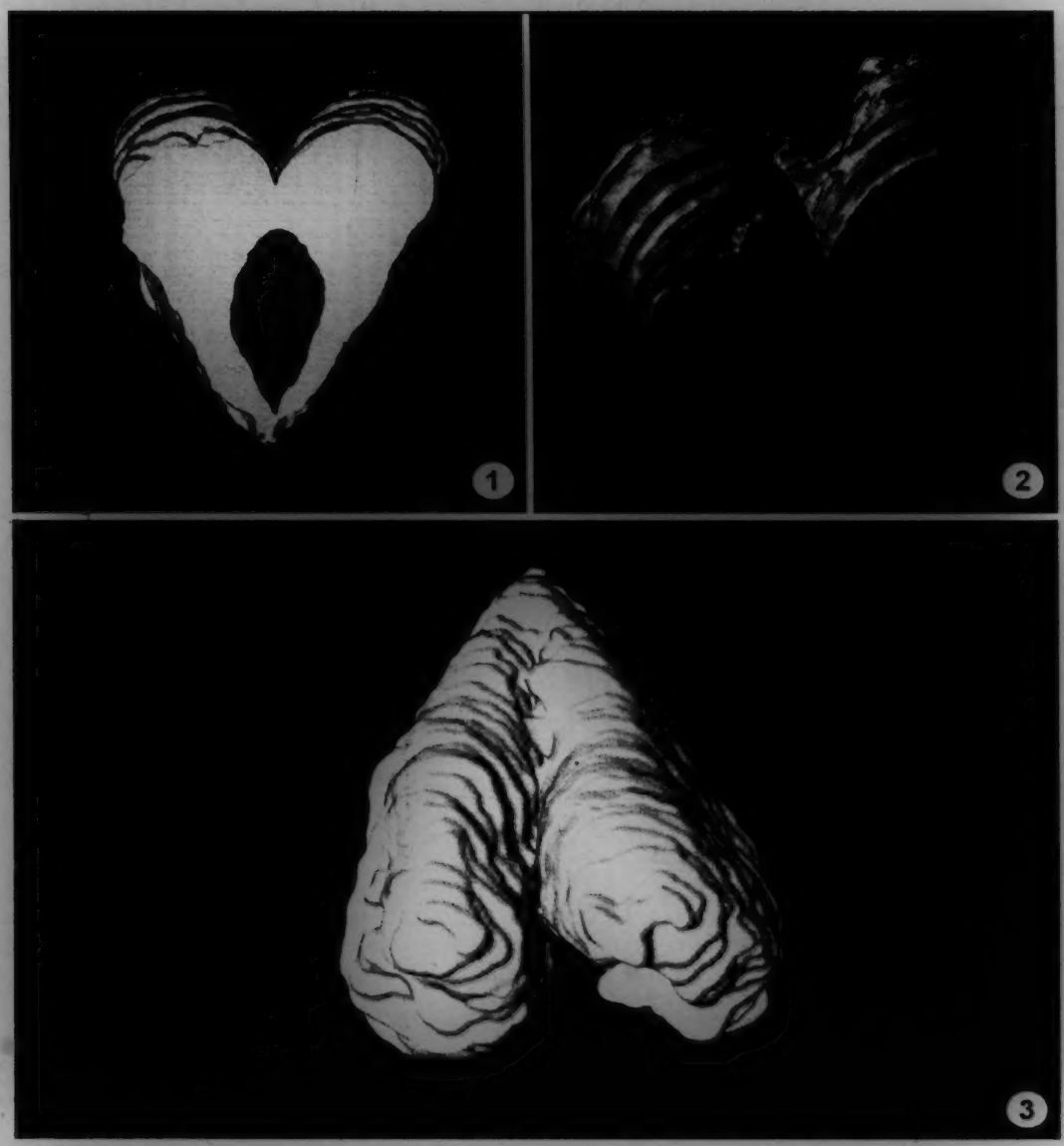
Plate 35

Figs. 1-3. Three dimensional reconstruction of heart-shaped mericarp (unknown fruit 12) P14355 C top .

Fig. 1. Fruit on side of saw cut showing location of seed (dark gray) and pericarp (light gray).

Fig. 2. Fruit on side of saw cut showing seed (dark gray) and lobed nature of wings.

Fig. 3. Fruit on opposite side of saw cut showing winged pericarp.


1
2
3

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